USE OF STOMACH TEMPERATURE TELEMETRY TO QUANTIFY INGESTION BY PHOCID SEALS

APRIL HEDD

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by

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A thesis submitted to the School of Graduate Studies in partial fulfilment of the requirements for the degree of Master of Science

Biopsychology Programme
Departments of Biology and Psychology
Memorial University of Newfoundland
August 1994

St. John's Newfoundland

ISBN 0-612-13904-2

Abstract

The applicability of using stomach temperature probes to investigate the feeding behaviour of seals was tested. Captive harp seals (Phoca groenlandica) were fed stomach temperature sensors and given pre-weighed meals of herring (Clupea harengus) and crushed ice. Ingestion of either substance caused a decrease in stomach temperature (see also Gales and Renouf 1993). Results suggested that the magnitude of stomach temperature change could indicate whether the ingested substance was a prey item or ice. The duration of stomach temperature change was significantly related to the quantity of fish consumed, but it accounted for just 27% of the overall variation. This percentage was much less than the 71% reported by Gales and Renouf (1993), perhaps due in part to the larger sample size used in the present study. Prey temperature was a significant covariate in the relationship between meal mass and the corresponding duration of stomach temperature change, but, overall it added very little to predictive power. Both the magnitude and duration of the temperature change were related to the quantity of ice consumed, accounting for 69% of the variation. Subsequent modelling of this relationship, however, revealed that it was not robust. Monitoring the stomach temperatures of wild seals would tell us little about the quantity of prey consumed, however, when used in conjunction with satellite-linked time-depth recorders they could provide valuable information on the location, timing and frequency of prey consumption.

A harbour seal (Phoca vitulina) mother and pup were fed stomach temperature probes throughout the lactation period. Behavioural observations were conducted while stomach temperature was concurrently logged. Milk intake caused a decrease in the pup's stomach temperature, and the duration of this temperature change was related to the length of the nursing bout. Laboratory stomach simulations, which suggested a strong relationship between milk volume and the subsequent duration of temperature change, were used to estimate the volume of milk consumed by the pup. Suckling bout length and the estimated milk intake per bout increased as a weekly average over the five week lactation period. A temporal change in the suckling pattern was noted, with a progression from largely nocturnal to daytime feedings. Although not visually confirmed, temperature data collected from the mother provided evidence of seawater ingestion. Direct pup feeding experiments using known quantities of the mother's milk, at a known temperature, would greatly improve the accuracy of these intake estimates.

These studies indicate that, with sufficient samples, stomach temperature probes may provide a valuable tool for investigating lactation energetics and other aspects of the feeding ecology of marine endotherms.

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Acknowledgements

I would first like to thank my supervisor, the late Dr. Deane Renouf. Her devotion, intellect and kindness were an inspiration to everyone who knew her, and her courage will never be forgotten. I thank her for the lessons in life she taught us all.

I would also like to thank Dr. Rosemary Gales for being available, above and beyond the call of duty, whenever I needed help. Her words of encouragement and her friendship were a great source of support. I am very grateful to Ransom Myers for providing statistical advice. The comments and suggestions of my Supervisory Committee - Drs. William Montevecchi (Acting Supervisor), Gene Herzberg, John Lawson and Garry Stenson - have greatly improved the quality of this work. I thank them all.

This project could have never been completed without the help of many people. Elizabeth Noseworthy, Patricia Dunphy, Grant Dalton, Dave Rosen, Jason Noseworthy, Megan Jones, Yolanda Rideout, and Miranda Hurry helped with data collection and processing. Craig Tuck and Dr. Denis Chabot developed computer programs which greatly facilitated the data analysis. I am very grateful to them all.

Special thanks to my husband, Lee Hedd, whose love and understanding have helped me immeasurably throughout the writing of this thesis. Finally, I thank my parents, David and Violet Lundrigan, for their love and support through the years.

1.0 Chapter 1

General Introduction

Pinnipeds are a diverse group of aquatic mammals consisting of the families Phocidae (true seals), Otariidae (fur seals and sea lions) and Odobenidae (the walrus). Although highly specialized for an aquatic lifestyle, these groups remain tied to either land or ice for breeding, moulting and raising their pups. In contrast to cetaceans, which are exclusively aquatic, the terrestrial requirements of pinnipeds have facilitated research into aspects of maternal investment (Trillmich 1986; Stewart 1987; Higgins et al. 1988; see Kovacs and Lavigne 1992 for a review of otariids and walruses), the energetics of lactation and moult (Fedak and Anderson 1982; Costa et al. 1986; Bowen et al. 1992; Worthy et al. 1992; Boyd et al. 1993; Oftedal et al. 1993), the ontogeny of behaviour (Lawson and Renouf 1987; Kovacs 1987a, 1987b; Rosen 1991) and behavioural aspects of reproduction (McCann 1980; Lawson and Renouf 1985; Le Boeuf 1986; Amos et al. 1993). While a large amount of data has been collected during periods when pinnipeds are on land, relatively little is known of their behaviour at sea.

This situation is problematic as in recent years much attention has been paid to the interaction of pinnipeds and commercial fisheries throughout the world (Harwood and Croxall 1988; Gales et al. 1993). Harwood and Croxall (1988) review the information necessary to assess such interaction: data on spatial and temporal distributions of predator and prey species; estimates of population size;

the type, quantity, and size of prey taken by seals and fisheries; and behavioural responses of all relevant groups to dynamic changes in resource availability.

The use of satellite-linked time-depth recorders has improved our understanding of the daily and seasonal distribution and movements of pinnipeds, including their behaviour at sea. The proportions of time spent resting, travelling, and foraging have been inferred from diving profiles, and provide some insight into the foraging ecology of seals (Le Boeuf et al. 1988; Hindell et al. 1991; Le Boeuf et al. 1992). This study was undertaken to calibrate a technique which may make it possible to directly investigate aspects of the feeding behaviour of wild seals.

Feeding behaviour has commonly been inferred from dive records, although until recently no direct method existed for detecting prey ingestion. Wilson et al. (1992) developed an archival unit that could be placed in the stomach and was capable of detecting and storing changes in temperature. It was reasoned that since the body temperature of marine prey items would, in most cases, be lower than that of the marine endotherm's stomach, ingestion could be indicated by a decrease in stomach temperature. Data were reported from captive African penguins (Spheniscus demersus) intubated with seawater, and from free-ranging wandering albatrosses (Diomedea exulans) carrying the loggers. Seawater ingestion by the penguins caused precipitous drops in stomach temperature followed by exponential recoveries to the pre-ingestion temperature levels (Wilson et al. 1992). Profiles of similar shape were obtained from albatrosses while at sea,

and were assumed to indicate instances of prey consumption. The integral of the temperature curve, which outlined the progression of stomach temperature change subsequent to ingestion, was used to estimate the mass of prey consumed by these birds. Stomach temperature sensors have since been used to determine the daily feeding patterns of other free-ranging wandering albatrosses (Weimerskirch and Wilson 1992), and to examine foraging depth in relation to success for a number of penguin species (Wilson et al. 1993).

Gales and Renouf (1993) investigated the use of stomach temperature telemetry to detect and measure food and water intake in captive harp seals (Phoca groenlandica). VHF temperature transmitters were used to record changes in stomach temperature as seals consumed ice, snow, seawater, and pre-weighed meals of herring (Clupea harengus). Ingestion was followed by a rapid decrease in stomach temperature. They found that the duration of stomach temperature change following meals of herring was related to the mass of prey eaten.

This thesis further examined the efficacy of stomach temperature sensors for detecting and estimating the feeding behaviour of captive seals, for possible application to studies of their wild counterparts. The main objective of the first portion of the study was to further calibrate the technique for quantifying food intake by harp seals. Wilson et al. (1992) concluded that estimates of the mass of prey ingested by free-ranging birds could be calibrated if changes in stomach temperature were examined after animals were fed meals of known mass and

temperature. Gales and Renouf (1993) also speculated that prey temperature along with feeding duration and frequency would effect the predictive relationships they found between meal mass and the rate of stomach temperature recovery. These questions were examined by feeding known masses of herring and crushed ice to captive harp seals.

In the second part of this study, a captive harbour seal (Phoca vitulina) mother and her pup were fed stomach temperature probes during the lactation period. This study represents the first attempt to use this technology to monitor milk intake by seals. Given the preliminary nature of the study, coupled with its small sample size, this aspect of the study was more concerned with investigating and attempting to calibrate the technique than in making any fundamental statements about the biology of lactation in harbour seals. The first and foremost objective of this section of the work was to determine if nursing bouts could be identified from changes in stomach temperature, and if so, to determine whether a relationship existed between the duration of a suckling session and the subsequent length of stomach temperature change. The possibility of using remote sensing to detect milk intake and thereby to provide a means with which to document ontogenetic changes in the temporal aspects of suckling behaviour was also investigated.

2.0 Chapter 2

Use of Stomach Temperature Telemetry to Estimate Prey Consumption by Harp Seals (Phoca groenlandica)

2.1 Introduction

Marine birds and mammals (seals and whales) are significant predators in marine ecosystems. In order to assess the role of these predators in marine food webs, rates of food consumption coupled with information on diet and population size must be obtained (see Chapter 1). Various methods have been used to estimate the type and quantity of food consumed by marine endotherms, but perhaps the most widely used techniques to date have been those of faecal and stomach content analysis. The rate of labelled-water turnover, serial changes in mass, and extrapolation from studies of food intake and energy expenditure of captive animals have also been used to estimate the energy consumption of wild populations.

As discussed in Chapter 1, recent technological developments such as the satellite-linked time-depth recorder and devices capable of recording changes in stomach temperature have vastly improved our ability to understand the movement and behaviour patterns of marine endotherms (Le Boeuf et al. 1988; Hindell et al. 1991; Le Boeuf et al. 1992; Wilson et al. 1992; Gales and Renouf 1993; Weimerskirch and Wilson 1993; Wilson et al. 1993).

This study tests the efficacy of using stomach temperature probes to both

detect and to quantify harp seal feeding behaviour, and provides the necessary calibration prior to using this technology to study the feeding ecology of free-living seals. The effects of feeding duration and prey temperature on the predictive relationships between meal mass and the rates of stomach temperature recovery were also investigated.

2.2 Methods and Materials

Seven captive harp seals (3 adult females, 2 adult males and 2 juveniles - 1 male and 1 female) housed at the Ocean Sciences Centre, Memorial University of Newfoundland, were used as subjects. The outdoor facility consisted of two tanks (12.3 metres in diametre, and 2.5 metres deep) filled with ambient temperature seawater pumped continuously at a rate of 200 litres/minute from the adjacent ocean. The tanks were surrounded by approximately 190 m^2 of wooden decking on which the seals could haul-out.

For two hours in the middle of each day the seals were fed ad libitum on thawed herring, the temperature of which varied from a low of -5.3 °C to a high 17.3 °C. Temperature-sensitive VHF transmitter probes (Biotrack, Dorset, UK) were concealed inside the herring and fed to the seals. The probes were retained for periods ranging from 1 to 267 days. Crushed ice was fed opportunistically either early in the morning or late in the afternoon; at such times the stomach was likely to be empty and its temperature uninfluenced by digestion (Markussen 1993).

Data were collected between 14 April, 1992 and 23 July, 1993.

The transmitters were housed in watertight plastic cylinders (51.3 millimetres long, 17.7 millimetres wide, weighing 11g). Pulses were received with a 2 or 3-element Yagi antenna and logged by a Lotek receiver (SRX 400; Lotek Engineering Inc., Aurora, Ont.). The transmitters were calibrated in a 4 litre waterbath prior to and following their administration to the seals. Sensors were maintained for 15 minutes at each 5 °C interval between 0 and 40 °C and their precision was determined to be within ± 0.2 °C of the waterbath temperature. Sensors responded to changes in temperature within 1 minute. Curve-fitted polynomial equations were used to derive stomach temperature from logged pulse durations.

For days on which the animals carried stomach transmitters, the time when they consumed their first and final fish was recorded, as were the temperatures of subsamples of these fish. and the meal mass. Similarly, when crushed ice was fed the beginning and end of the feeding session, as well as the mass of the ice consumed, was recorded.

Temperature changes in response to the ingestion of ice or fish were analyzed according to 3 operationally-defined points (as in Gales and Renouf 1993): A) the time of departure from stable temperature prior to a meal, B) the time at which stomach temperature reached its minimum during the meal, and C) the time at which a stable temperature to within ± 0.2 °C of A was reached

following the meal. In an attempt to incorporate all temperature changes in a single parametre, the area enclosed by the temperature curve and bounded by points A-C was calculated using a program written in MS-DOS QBasic (Microsoft Corp., USA) software version 5.0. As the curve defining changes in stomach temperature was not strictly linear, area was calculated in a number of sections in a manner such that errors in area estimation were less than 5% of the calculated total. A number of the parametres used to characterize the changes in stomach temperature following food intake were non-normally distributed. In such cases, data were log-transformed prior to analysis, and checked for normality with Kolmogorov-Smirnov tests.

Many of the receiver's filter settings were disabled in order to increase the probability of receiving valid temperature points. As a result extraneous data points were often logged (Figure 1). The operationally-defined points (A,B,C) were first determined visually from the raw data.

To test the validity of this approach results from a subset of the data (n = 27) were compared to those obtained when the points (A,B,C) were derived from data which had been passed through a custom temperature filtering procedure (D. Chabot, Department of Fisheries and Oceans, Mont-Joli, Quebec, Canada). Initially, double-intervals (double-beats) were corrected to valid interval durations. A valid interval duration was determined by examining the first 10 lines of each file and entering the most frequently occurring pulse duration. Temperature was then

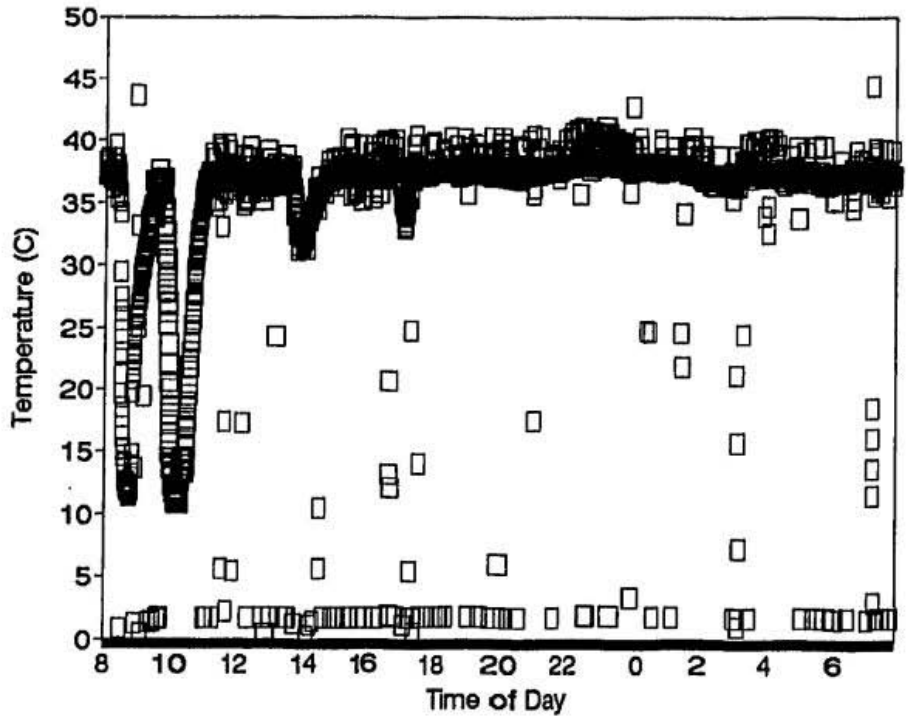


Figure 1: Example of raw telemetry recordings obtained from an adult female harp seal during September of 1992.

calculated using the polynomial equations derived from the calibration curve for that transmitter. The data were then scanned visually for feeding episodes, and any remaining temperatures which were lower than the lower limit caused by feeding were deleted. For example, in Figure 1 temperatures below 10 °C were deleted at this point. The remaining data were subjected to a filtering routine. A valid entry temperature was chosen (one which fell within the range of expected mammalian body temperatures 36 - 38 ° C; Schmidt-Nielsen 1983) from the first 10 lines of a particular file. Routines were implemented which compared each temperature to the average of the previous 4 points, the point itself, and the subsequent 4 points. The number of subsequent points included in the average depended on the level of noise in the data. Each filtering routine used rules based on the standard deviation of the mean temperature in deciding whether or not a point was excluded. That is, decisions changed through time dependent on trends in the data, and such trends were indicated by a changing standard deviation. The advantage of routines which examined data both prior to and subsequent to any particular point was that they could deal with diel cycles in body temperature or changes in temperature due to feeding (D. Chabot, personal communication). Figure 1 provides an example of raw telemetry recordings, and Figure 2 shows the same file after it had been passed through the filtering procedure, with the relative positions of points A, B and C indicated. The durations of stomach temperature change (A-C) obtained from the filtered and unfiltered temperature files were not

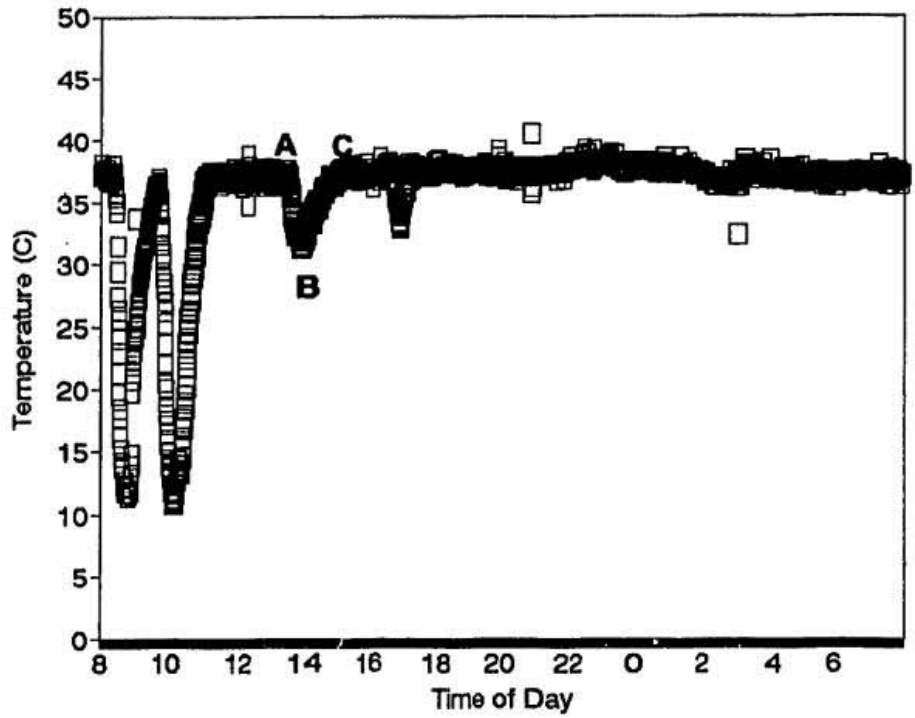


Figure 2: The telemetry data presented in Figure 1 after it had been passed through the filtering procedure. The relative points of A,B and C are indicated.

significantly different (Kruskal-Wallis one-way ANOVA; $p > 0.05$).

The various parametres characterizing changes in stomach temperature following feeding were used in both linear and multiple regression analyses to assess the influences of the quantity of fish or ice ingested. There are varying opinions in the statistical literature regarding which variable should be treated as independent and dependent in linear regressions of calibration data (Williams 1959; Krutchkoff 1967; Martinelle 1970). It is arguable whether the regression should be calculated according to the equation $y = a + bx$ (where, in this case, y would be the particular stomach temperature parametre, and x the meal mass; called the classic approach) or according to the equation $x = c + dy$ (where, x would be the meal mass, and y the stomach temperature parametre; called the inverse approach). Krutchkoff (1967) identifies the inverse approach as superior due to its uniformly smaller mean squared error. However, Martinelle (1970) concludes that this method is superior only when the sample size is small. Further, Williams (1959) states that in simple regressions of calibration data, where both variables are subject to error (or where both are measured accurately), that either the classic or inverse method may be used, and choice should depend upon which variable is to be later predicted. Because in this situation both the changes in stomach temperature and the meal masses were measured with little error, both classic and inverse regressions were provided where appropriate. Statistical analyses were performed using NCSS (Number Cruncher Statistical

System, Kaysville, Utah) software version 5.03 and the Curve Fitter program 5.9. Means and standard deviations were provided as appropriate, and probability levels of less than 5% were accepted as statistically significant.

2.3 Results

Stomach temperature data were obtained during 68 meals of fish and 29 instances of ice consumption. Table 1 provides a breakdown of the number of meals of both fish and ice eaten by individual seals. Figure 3 illustrates a stomach temperature profile obtained from an adult female harp seal, during which she consumed measured quantities of herring and crushed ice. Points A, B, and C are indicated on this graph.

Meals of herring consumed during periods when stomach temperatures were logged ranged from 514 to 7591 g, while masses of ice consumed ranged from 53 to 7618 g (Tables 2 and 3). Ingestion of either fish or ice was followed by a decrease in stomach temperature. The overall magnitude of this temperature change (A-B) was greater when meals of ice were consumed (21.2 ± 8.6 ° C for ice versus 5.5 ± 2.2 ° C for fish; Kruskal-Wallis one-way ANOVA, $H = 41.5$, $df = 1$, $p < 0.001$).

2.31 Herring Experiments

Linear regressions indicated that just three of the five stomach temperature

Table 1

Breakdown of the number of meals of fish and ice eaten per individual animal (A = adult; J = juvenile; M = male; F = female)

Sex and Age of the Individual	Number of meals of Fish	Number of meals of Ice
AF1	19	11
AF2	18	4
AF3	2	1
AM1	10	0
AM2	12	4
JF1	2	5
JM1	5	4

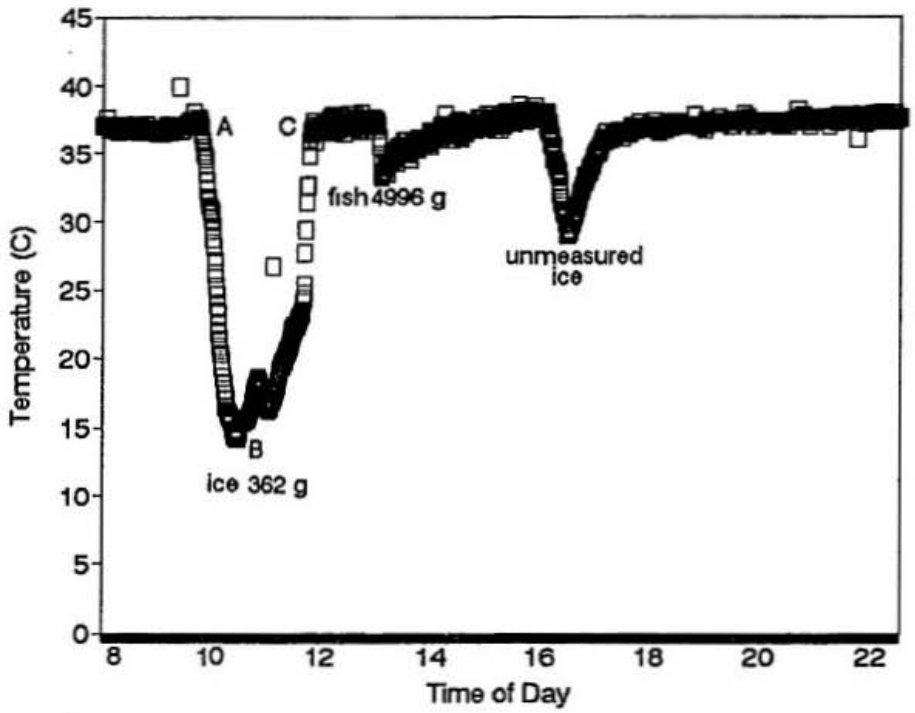


Figure 3: Stomach temperature profile obtained from an adult female harp seal on 30 September, 1992. Measured quantities of crushed ice and herring were fed while stomach temperature was continually logged. The relative positions of points A,B, and C are given. These data have undergone the filtering procedure.

Table 2

Descriptive statistics of variables obtained from the herring experiments

Variable	n	Mean	Standard Deviation	Range
Meal Mass (g)	68	4733.8	1635.6	514 - 7591
Fish Temperature (°C)	68	6.8	5.4	-5.3 - 17.3
Log of Area Under the Curve	68	5.3	0.5	4.0 - 6.4
Log of A to B (Minutes)	68	2.3	0.4	1.1 - 3.3
Log of A to B (Temperature,°C)	68	1.6	0.4	0.9 - 2.7
Log of B to C (Minutes)	68	4.7	0.4	3.6 - 5.5
Log of A to C (Minutes)	68	4.8	0.4	3.8 - 5.6
Length of Feeding (Minutes)	67	59.1	30.3	1 - 116

Table 3

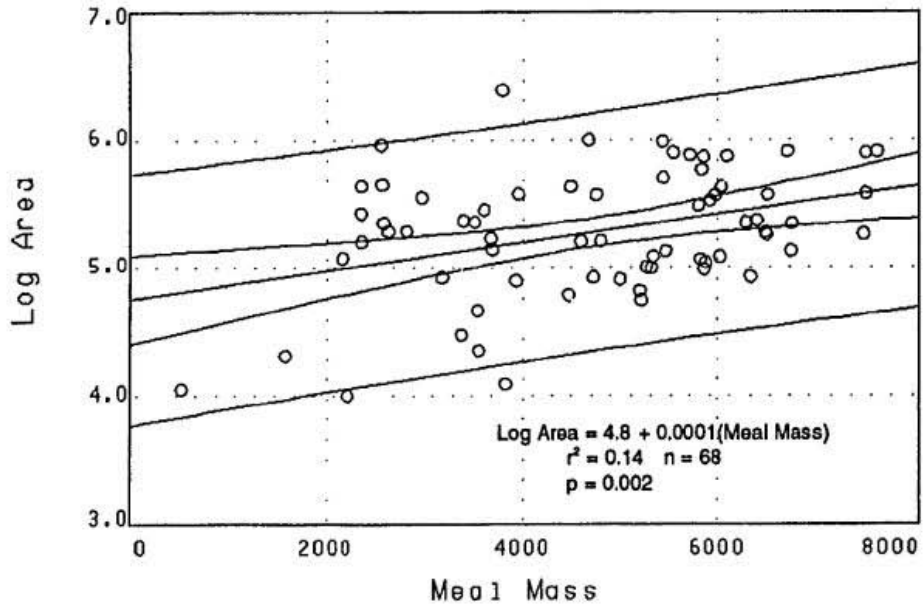
Descriptive statistics of variables obtained from the ice experiments

Variable	n	Mean	Standard Deviation	Range
Log of Meal Mass (g)	29	6.2	1.3	4.0 - 9.0
Log of Area Under the Curve	23	5.7	0.9	3.4 - 7.5
Log of A to B (Minutes)	27	2.0	0.7	0 - 3.0
A to B (Temperature, °C)	27	21.2	8.6	2.9 - 32.2
B to C (Minutes)	27	42.1	17.2	19 - 87
Log of A to C (Minutes)	29	3.9	0.5	3.0 - 4.8
Log of Length of Feeding (Minutes)	29	1.9	0.9	0 - 3.9

parametres (Log Area, Log A-C, Log B-C) were significantly related to the quantity of food consumed. Although significant, the proportion of meal mass variability accounted for was low, and for each parametre it was less than 30%. Both classic and inverse regressions of these data are provided in Figures 4-6. In all cases, the proportion of variance accounted for by the two regression methods was equivalent, and the confidence limits on predictions were equally wide.

Due to the limited predictability generated from regressing individual temperature parametres upon meal mass, all variables summarized in Table 2 (with the exception of mass itself) were used in multiple regression analyses. Entering all variables listed in Table 2 into a multiple regression analysis accounted for 50% of the variance in the mass of herring fed to the seals ($F_{(7,59)}=8.29$, $p < 0.001$). As metabolic rate in harp seals has been shown to vary with season, age, sex and reproductive status (Renouf and Gales 1994), data were partitioned and analyzed accordingly. Table 4 lists the results of stepwise regression analyses performed on the fish consumption data. A statistically significant prediction of meal mass was possible in all cases, but the proportion of variance accounted for in each analysis varied widely (44-86%). The length of feeding was a significant predictor in six of the seven analyses, followed by the temperature of the fish, which occurred in four of the predictive equations. Log of the area under the temperature curve and the log of the time from B-C appeared in three of the equations, whereas the log of the time and log of the temperature from A-B were

a.



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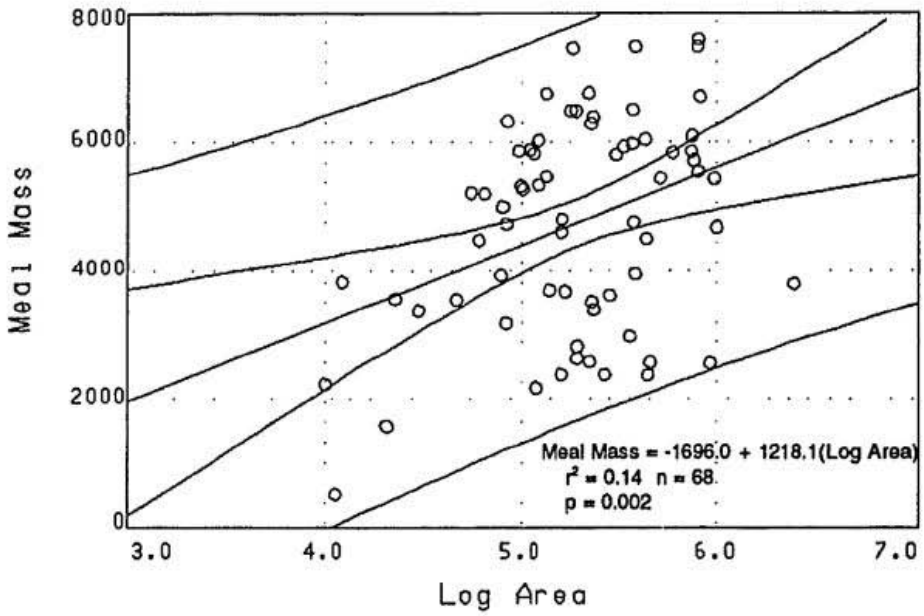


Figure 4: a) Classic and b) Inverse regression of the Log of Area and Meal Mass for the herring experiments. Confidence Intervals for the mean (lines closest to the regression line) and for the individual predictions (lines furthest from the regression line) are shown.

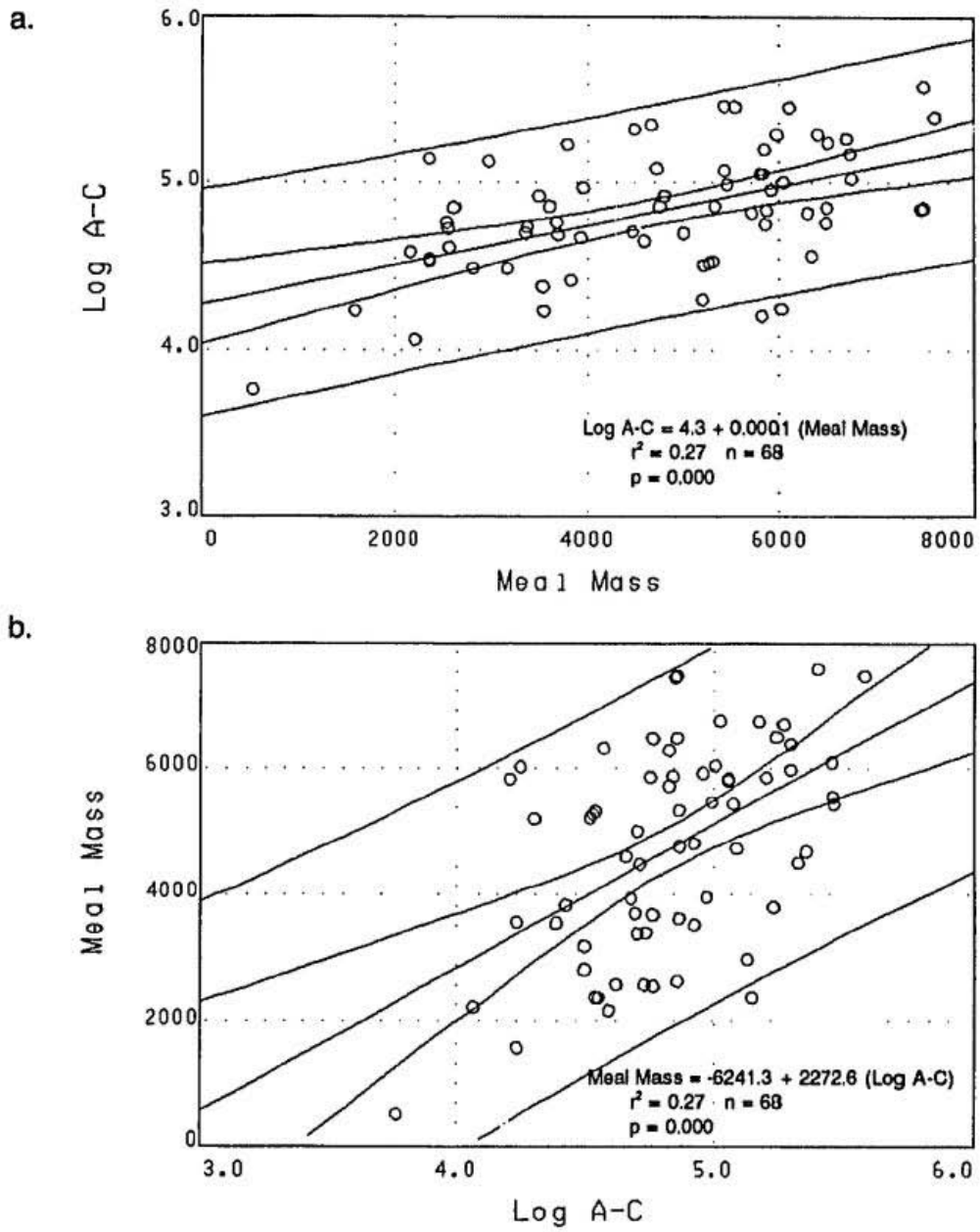


Figure 5: a) Classic and b) Inverse regressions of the Log of A-C (min) and Meal Mass for the herring experiments. Confidence intervals for the mean (lines closest to the regression line) and for individual predictions (lines furthest from the regression line) are shown.

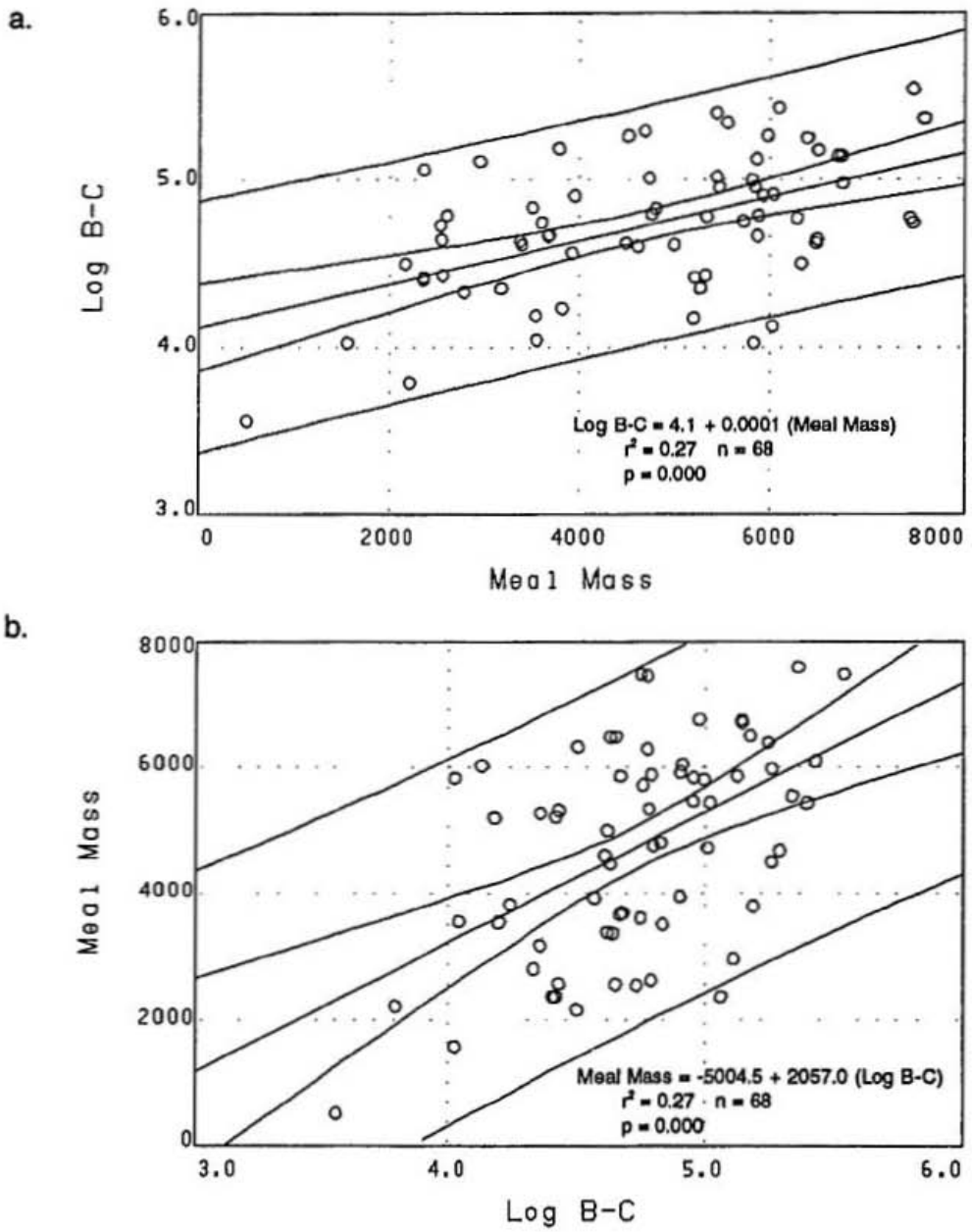


Figure 6: a) Classic and b) Inverse regressions of the Log of B-C (min) and Meal Mass for the herring experiments. Confidence intervals for the mean (lines closest to the regression line) and for individual predictions (lines furthest from the regression line) are shown.

Table 4
Results of stepwise regression procedures for predicting the mass of herring consumed by harp seals using all available variables {Log of area under the curve, Log of A-B (min), Log of A-B (temp); Log of B-C (min), Log of A-C (min), fish temperature, and length of feeding (min)}. Analyses were performed using the entire data set, as well as when the data were partitioned by season, age and sex of the subjects.

Data Analyzed	F Ratio p level	n	Intercept (±SE)	Co-Efficients (±SE)	Variable(s)	r^2
All Data	$F_{(3,63)} = 19.1$ $p < 0.001$	67	-3951.3 (1874.5)	85.2 (27.7) 20.7 (5.7) 1449.0 (417.9)	Fish Temp Lgt Feeding Log B-C min	0.48
Summer (April-September)	$F_{(3,43)} = 21.6$ $p < 0.001$	47	-3331.5 (1901.9)	117.4 (31.3) 28.9 (5.6) 1057.9 (378.7)	Fish Temp Lgt Feeding Log Area	0.60
Winter (October-March)	$F_{(3,16)} = 7.8$ $p < 0.01$	20	-4161.9 (4302.5)	3516.5 (1029.1) -907.8 (744.4) -4671.7 (1031.5)	Log Area Log A-B min Log A-B temp	0.59
Adults	$F_{(3,56)} = 16.7$ $p < 0.001$	60	-2534.5 (1939.2)	58.6 (29.8) 24.4 (5.7) 1177.6(426.1)	Fish Temp Lgt Feeding Log B-C min	0.47
Juveniles	$F_{(2,4)} = 12.1$ $p < 0.05$	7	-909.4 (1313.4)	27.3 (5.8) 969.4 (487.4)	Lgt Feeding Log A-B min	0.86
Adult Males	$F_{(3,17)} = 26.3$ $p < 0.001$	21	-3337.5 (2029.7)	79.8 (43.8) 38.5 (5.3) 1114.3 (388.7)	Fish Temp Lgt Feeding Log Area	0.82
Adult Females	$F_{(3,35)} = 9.2$ $p < 0.001$	39	-4547.33 (2597.4)	13.5 (8.3) -928.8 (670.2) 2070.5 (599.0)	Lgt Feeding Log A-B temp Log B-C min	0.44

both significant predictors in two of the analyses.

Table 5 lists the results of stepwise regression analyses for predicting meal mass using only those variables which would be available from a free-ranging animal; the length of feeding and fish temperature have been excluded. When all variables were entered into a regression analysis, 28% of the meal mass variation was accounted for ($F_{(5,62)}$=4.94, $p < 0.01$). Although in six of the seven stepwise analyses a significant prediction of meal mass was still possible, in most cases, the proportion of variance accounted for decreased relative to the results in Table 4 and ranged from 24-80%. With the length of feeding and fish temperature removed, the log of B-C in minutes was a significant predictor variable in four of the six analyses, while the log of A-B in temperature and the log of the area under the curve appeared in two of the six analyses. The log of A-C and A-B in min were both significant meal mass predictors in just one instance.

Although in Tables 4 and 5 many variables appear to be important inclusions in the predictive equations, log of the area under the curve, log of A-C in min, and log of B-C in min are of particular importance, as each alone is significantly related to meal mass (Figures 4-6). Table 6 shows the proportion of meal mass variance accounted for when each of these variables was sequentially forced into a regression analysis. In general, the addition of the parametres log of B-C in min and log of the area under the curve did not account for more of the meal mass variation than did log of A-C alone. The exceptions were when the

Table 5

Results of stepwise regression procedures for predicting the mass of herring consumed by harp seals using only those variables which would be available from free-ranging animals{Log of area under the curve, Log of A-B (min), Log of A-B (temp), Log of B-C (min), and Log of A-C (min)}. Analyses were performed using the entire data set, as well as when the data were partitioned by season, age and sex of the subjects.

Data Analyzed	F Ratio p level	n	Intercept (±SE)	Co-Efficients (±SE)	Variable(s)	r^2
All Data	$F_{(1,66)} = 24.0$ $p < 0.001$	68	-5004.5 (1993.6)	2057.0 (419.5)	Log B-C min	0.27
Summer (April-September)	$F_{(1,46)} = 16.5$ $p < 0.001$	48	-5504.3 (2483.4)	2179.0 (536.1)	Log B-C min	0.26
Winter (October-March)	$F_{(3,16)} = 7.8$ $p < 0.01$	20	-4161.9 (4302.5)	3516.5 (1029.1) -907.8 (744.4) -4671.7 (1031.5)	Log Area Log A-B min Log A-B temp	0.59
Adults	$F_{(1,59)} = 18.4$ $p < 0.001$	61	-4089.3 (2117.8)	1900.3 (443.5)	Log B-C min	0.24
Juveniles	$F_{(2,4)} = 8.0$ $p < 0.05$	7	-8546.0 (2927.6)	-781.4 (428.6) 3317.0 (1008.3)	Log Area Log A-C min	0.80
Adult Males	ns $p > 0.05$	-	-	-	-	-
Adult Females	$F_{(2,36)} = 11.9$ $p < 0.001$	39	-6086.4 (2478.0)	963.2 (685.4) 2572.5 (526.8)	Log A-B temp Log B-C min	0.40

Table 6

The proportion of variance accounted for (r^2) when three temperature file parameters {Log of A-C (min), Log of B-C (min), and Log of the area under the curve} were each sequentially entered into a regression analysis to predict meal mass. Asterisks indicate significant increments in r^2.

Data Analyzed	Log of A-C (min)	Log of A-C (min) and Log of B-C (min)	Log of A-C (min) Log of B-C (min) and Log of Area
All Data	0.27*	0.27	0.27
Summer (April-September)	0.25*	0.27	0.27
Winter (October-March)	0.23*	0.28	0.36*
Adults	0.23*	0.24	0.24
Juveniles	0.64*	0.66	0.82*
Adult Males	0.15	0.15	0.16
Adult Females	0.36*	0.37	0.37

data from juveniles and the data collected during winter were considered separately. In these cases, knowledge of log of the area under the curve added significantly to the predictive power of the log of A-C.

Possible covarying effects of fish temperature and the length of feeding were examined by partitioning the meals of herring into three groups (0-3, 3-5, and 5-8 kg; Table 7) and comparing them using analyses of variance and covariance with data for three significant predictor variables (log of A-C min, log of B-C min, log of the area under the curve; Table 8). Group differences were found in the duration of stomach temperature change (log of A-C, log of B-C) following meals of fish ($F_{(2,65)}$=5.70, $p < 0.01$; $F_{(2,65)}$=5.78, $p < 0.01$, respectively). Specifically, the duration of stomach temperature change was significantly longer for meals ranging from 5-8 kg than for those ranging from 0-3 kg (Fisher's LSD procedure, $p < 0.05$ for both analyses). No significant differences were found among the meal size groups with respect to area under the curve ($F_{(2,65)}$=2.65, $p > 0.05$).

With the effects of fish temperature removed, the log of the area under the curve was significantly different for meals of fish ranging from 0-3 kg and 5-8 kg ($F_{(2,64)}$=3.96 $p < 0.05$; Fisher's LSD procedure, $p < 0.05$). Fish temperature did not significantly effect either the log of A-C or the log of B-C. Using the length of feeding as a covariate did not result in more efficient tests of the dependent variables, despite the fact that it was, itself, a significant covariate in all three analyses (Table 8).

Table 7

Descriptive statistics for meals of herring when separated by mass.

Meal Mass	n	Mean (g)	Standard Error
0-3 kg	13	2284.8	177.74
3-5 kg	21	4027.1	139.84
5-8 kg	34	6106.7	109.90

Table 8

Results of Analyses of Variance and Covariance performed with and without the effects of covariates (fish temperature and length of feeding) removed from three different predictor variables. Meals of fish are categorized into 3 groups based on mass {0-3 kg (1); 3-5 kg (2); 5-8 kg (3)}. Post hoc comparisons were performed using Fisher's LSD procedure, with all indicated differences having $p < 0.05$.

Covariate Tested	Predictor Variable		
	Log of Area Under the curve	Log of A-C (Min)	Log of B-C (Min)
None	$F_{(2,65)} = 2.53$ $p > 0.05$	$F_{(2,65)} = 5.70$ $p < 0.01$ $1 \neq 3$	$F_{(2,65)} = 5.78$ $p < 0.01$ $1 \neq 3$
Fish Temperature (°C)	$F_{(2,64)} = 3.96$ $p < 0.05$ $1 \neq 3$	Covariate not significant	Covariate not significant
Length of Feeding (Min)	$F_{(2,63)} = 0.94$ $p > 0.05$	$F_{(2,63)} = 1.32$ $p > 0.05$	$F_{(2,63)} = 1.38$ $p > 0.05$

In order to develop and subsequently test a model for quantifying food intake, the data set was partitioned into two groups; the first was used to develop the model using stepwise regressions (see Table 9) and the second used to test its usefulness. The groups were formed by assigning all data collected on even-numbered Julian dates to one group, and those collected on odd-numbered Julian dates to a second group. Both groups were used, in turn, to both build and test the models. The proportion of meal mass variance accounted for by the two models was widely different. While model 1 accounted for just 17% of the meal mass variance, model 2 accounted for 59% of the variance. Results of the model tests are provided in Figure 7. Results were again variable. Model 1 was relatively efficient at predicting the actual quantity of food consumed ($r^2 = 0.50$), while model 2 provided much poorer predictions ($r^2 = 0.12$).

2.32 Ice Experiments

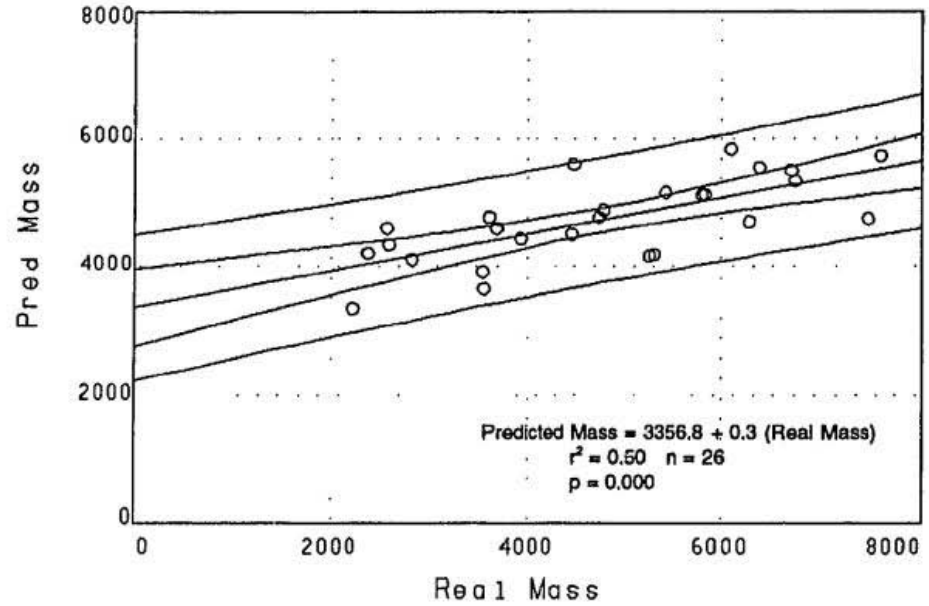
Descriptive statistics for the meals of ice consumed by the seals are presented in Table 3. Four of the five parametres characterizing stomach temperature changes (log of area under the curve, log of A-B min, log of A-C min, B-C min) were significantly related to the quantity of ice consumed. The proportion of ice mass variance accounted for by these individual parametres varied from 31-60%. Both classic and inverse regressions of these data are provided in Figures 8-11. Again, the proportion of variance accounted for by the two regression

Table 9

Two models developed from data sub-sets to predict the quantity of food consumed by harp seals from known changes in stomach temperature. Each set of data subsequently served to test the predictability of the alternate model.

Data used to create the model	n	Intercept (± SE)	Co-efficient (± SE)	Variable	r^2 and p level
Data gathered on even-numbered Julian days (Model 1)	42	-3915.9 (± 3067.1)	1786.2 (± 633.6)	Log A-C min	0.17 p < 0.01
Data gathered on odd-numbered Julian days (Model 2)	26	-6937.9 (± 2566.6)	-1526.4 (± 738.0) 4183.8 (± 858.2)	Log Area Log B-C min	0.59 p < 0.001

a.



b.

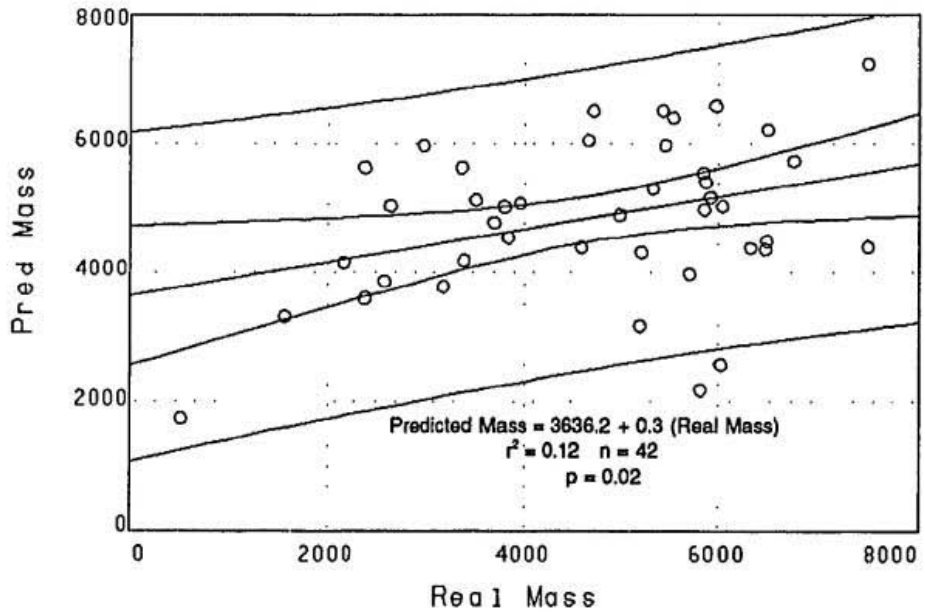
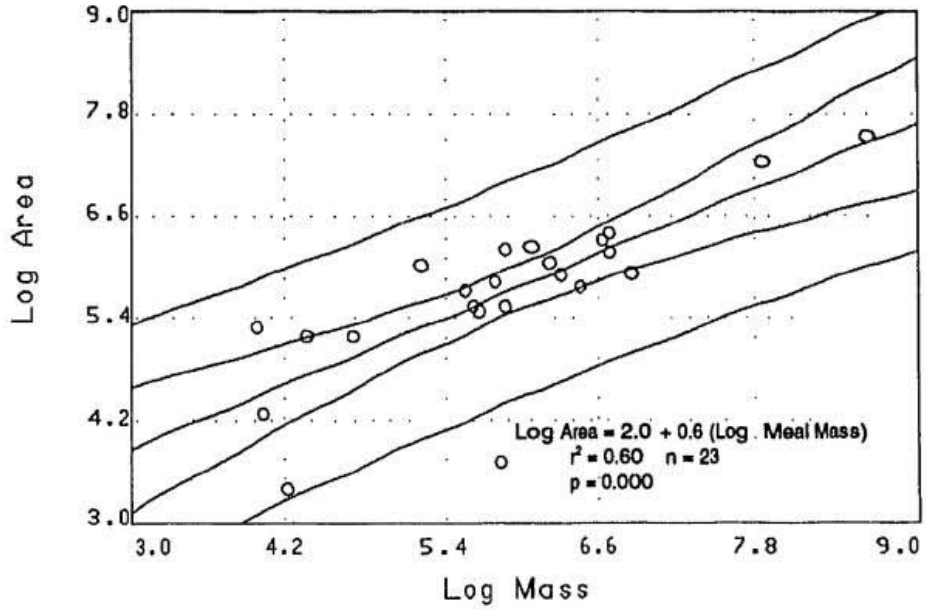


Figure 7: Predicted versus the actual mass of herring consumed by harp seals. a) Test of Model 1, and b) Test of Model 2. For model structure see Table 9.

a.



b.

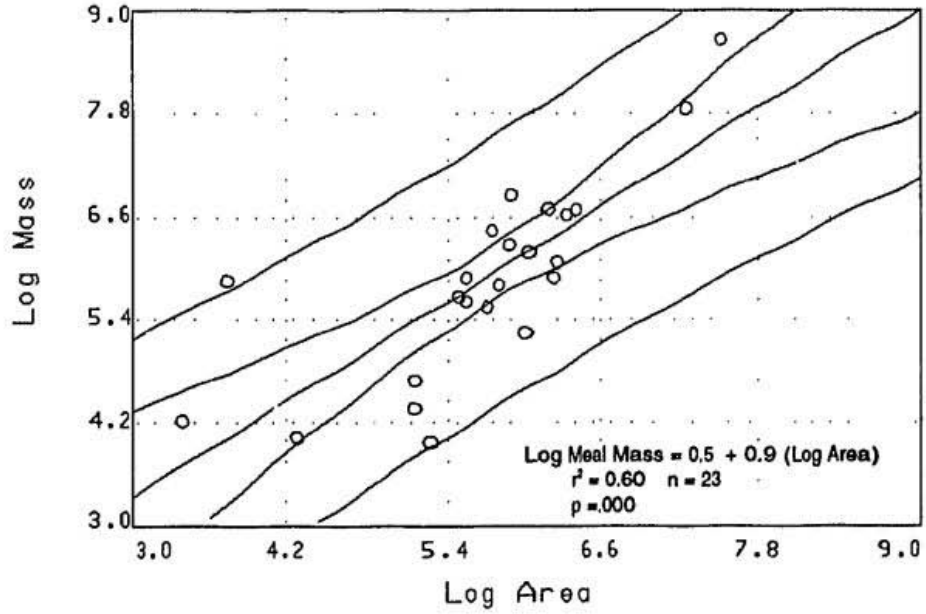


Figure 8: a) Classic and b) Inverse regressions of the Log of Area and the Log of Meal Mass for the ice experiments. Confidence intervals for the mean (lines closest to the regression line) and for individual predictions (lines furthest from the regression line) are shown.

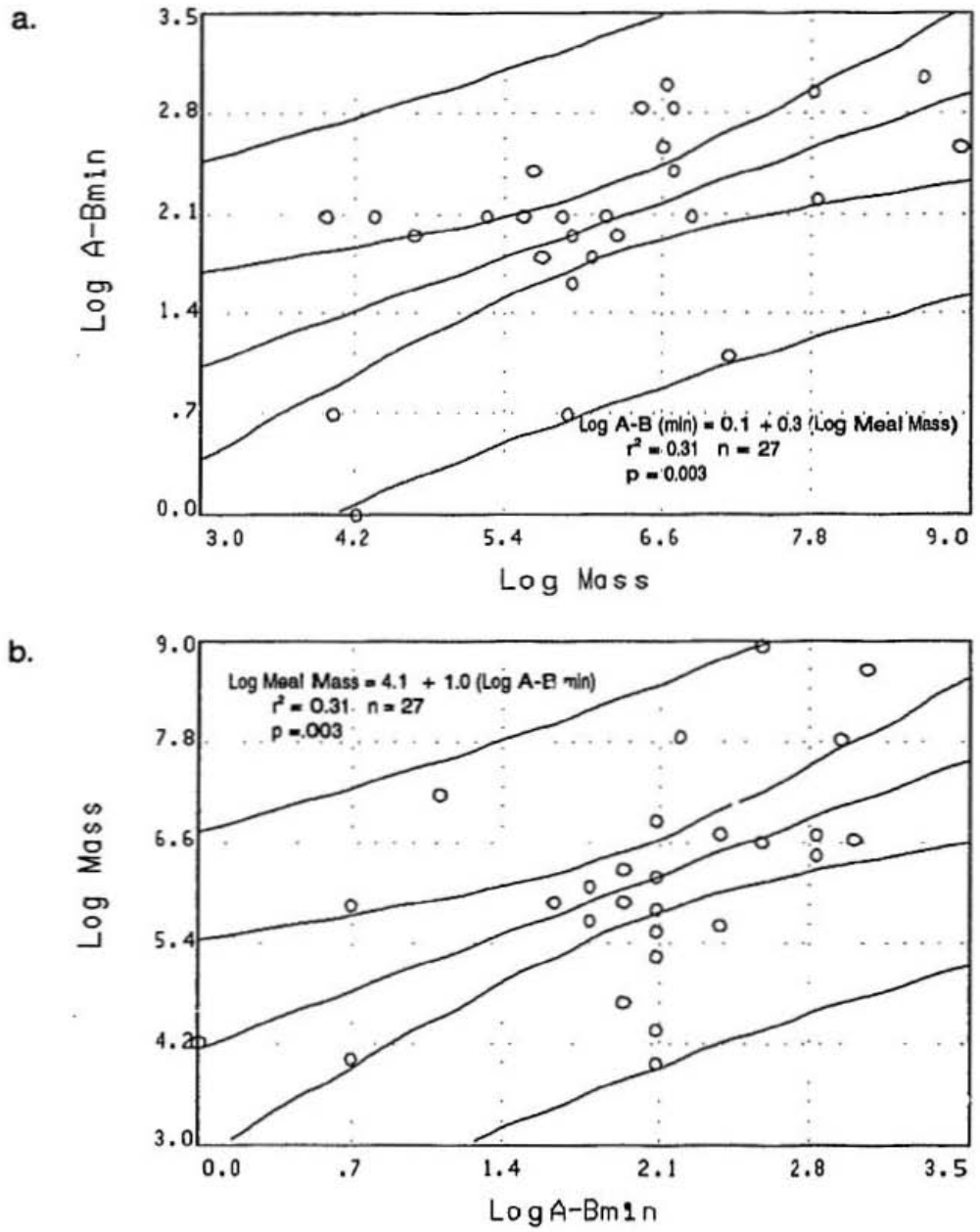
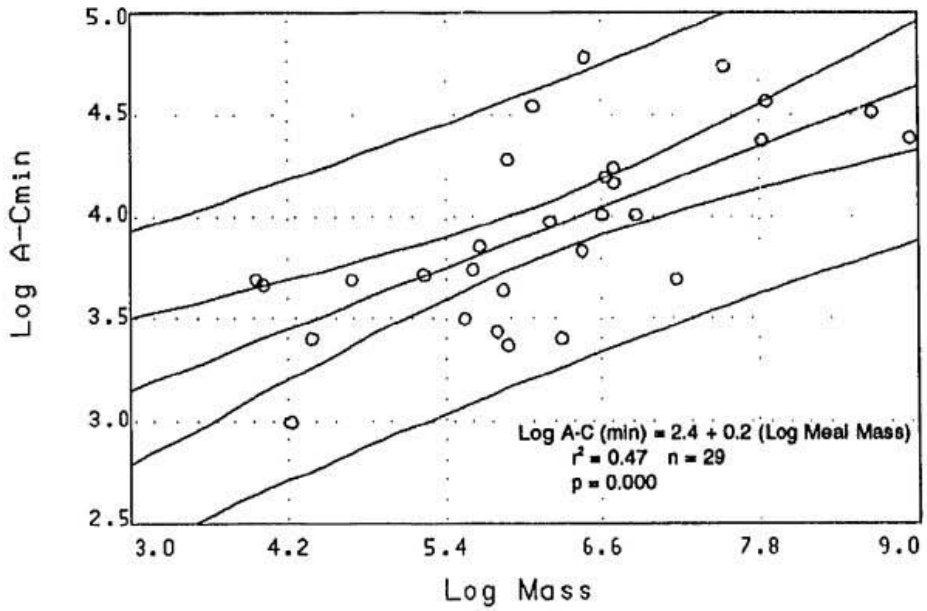


Figure 9: a) Classic and b) Inverse regressions of the Log of A-B (min) and the Log of Meal Mass for the ice experiments. Confidence intervals for the mean (lines closest to the regression line) and for individual predictions (lines furthest from the regression line) are shown.

a.



b.

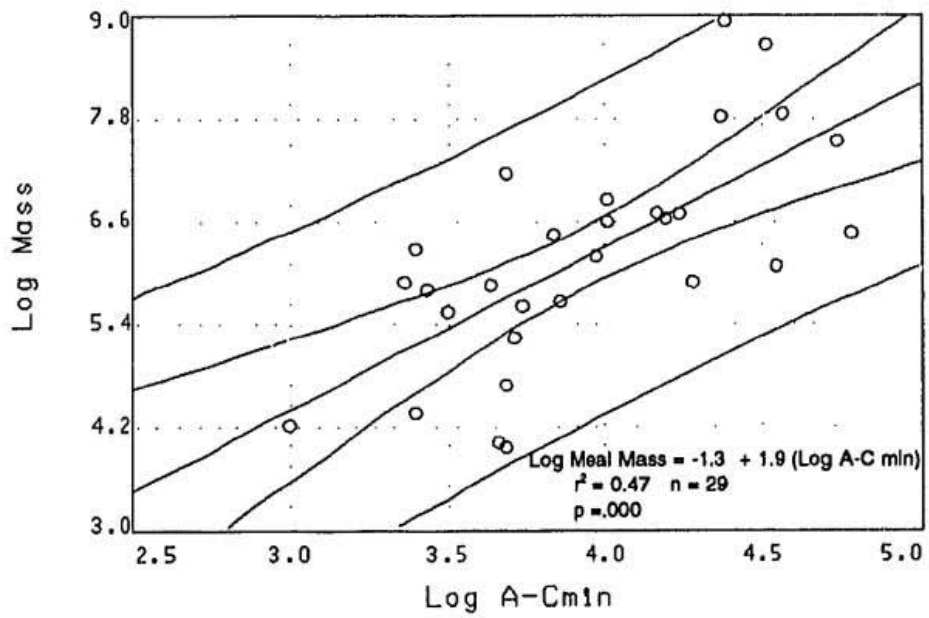
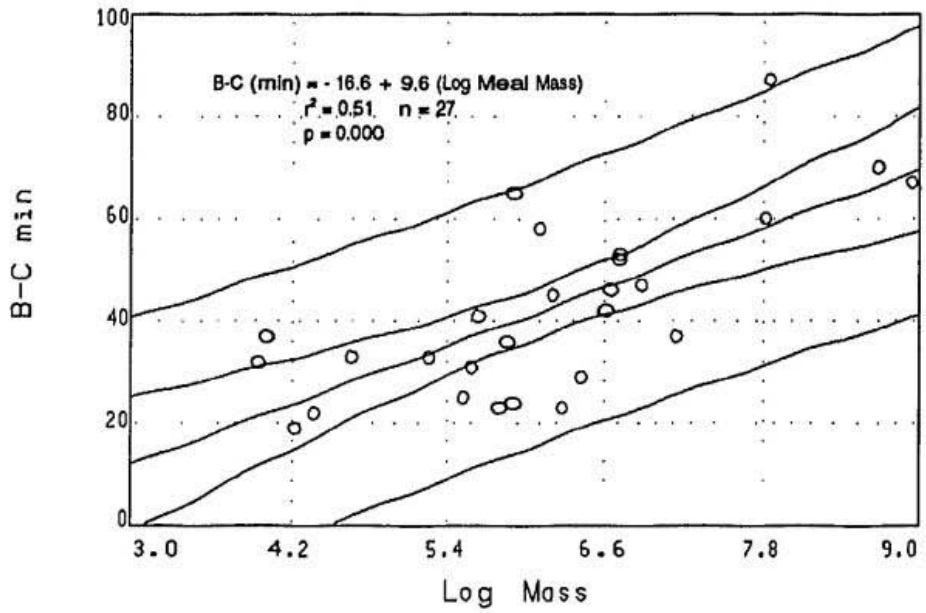


Figure 10: a) Classic and b) Inverse regressions of the Log of A-C (min) and the Log of Meal Mass for the ice experiments. Confidence intervals for the mean (lines closest to the regression line) and for individual predictions (lines furthest from the regression line) are shown.

a.



b.

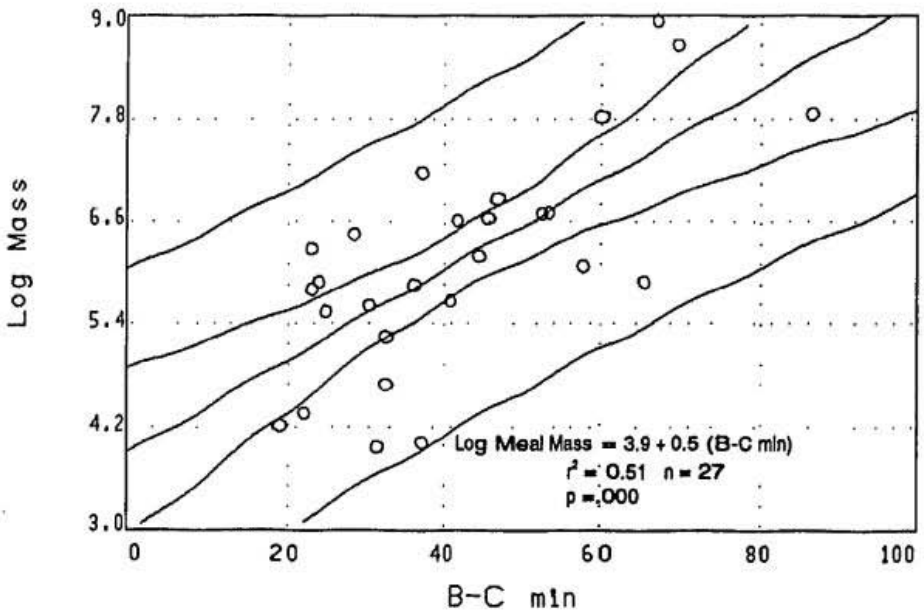


Figure 11: a) Classic and b) Inverse regressions of B-C (min) and the Log of Meal Mass for the ice experiments. Confidence intervals for the mean (lines closest to the regression line) and for individual predictions (lines furthest from the regression line) are shown.

methods was equivalent, and confidence intervals were of comparable widths.

Similar analyses to those outlined for herring were performed on the ice consumption data. When all variables were entered into a multiple regression analysis, 94% of the meal mass variability was accounted for ($F_{(6,16)}$=43.22, p < 0.001). Tables 10 and 11 list results of the stepwise regression procedures. As the data set was smaller in this case, it was subdivided by season only. When all variables were included, a significant prediction of the mass of ice consumed was possible in all cases. The log of the length of feeding was always a significant predictor variable. The log of the area under the curve was a significant predictor in two of the three analyses and the log of the time from A-B and the time from B-C were significant predictor variables in just one instance. The proportion of variance accounted for was large in all cases (89-94%; Table 10).

Table 11 provides the results for predicting ice consumption when all variables except the log of the length of feeding were included. When all remaining variables were entered into a regression analysis, 71% of the ice mass variability was accounted for ($F_{(5,17)}$ = 8.46, p < 0.001). When using stepwise analyses, significant predictions were possible for the data set as a whole, as well as for data from the summer months (April-September). The proportion of variance accounted for in these analyses was 69 and 78%, respectively. A-B in temperature, B-C min and the log of the area under the curve were the only significant parametres, each appearing in just one of the analyses.

Table 10

Results of stepwise regression procedures for predicting the mass of ice consumed by harp seals using all available variables {Log of area under the curve, Log of A-B (min), A-B temperature, B-C (min), Log of A-C (min), and Log of the length of feeding (min)}. Analyses were performed using the entire data set, as well as when the data were partitioned by season.

Data Analyzed	F Ratio p level	n	Intercept (±SE)	Co-Efficients (±SE)	Variable(s)	r^2
All Data	$F_{(3,19)} = 82.6$ $p < 0.001$	23	3.7 (0.2)	0.02 (0.005) -0.2 (0.1) 1.1 (0.1)	B-C min Log A-B min Log Lgt Feeding	0.93
Summer (April-September)	$F_{(2,13)} = 54.4$ $p < 0.001$	16	0.1 (1.1)	0.8 (0.2) 0.8 (0.2)	Log Area Log Lgt Feeding	0.89
Winter (October-March)	$F_{(2,4)} = 32.9$ $p < 0.01$	7	5.1 (0.5)	-0.2 (0.1) 1.0 (0.1)	Log Area Log Lgt Feeding	0.94

Table 11

Results of stepwise regression procedures for predicting the mass of ice consumed by harp seals using only those variables which would be available from free-ranging animals {Log of area under the curve, Log of A-B (min), A-B temperature, B-C (min), and Log of A-C (min)}. Analyses were performed using the entire data set, as well as when the data were partitioned by season.

Data Analyzed	F Ratio p level	n	Intercept (±SE)	Co-Efficients (±SE)	Variable(s)	r^2
All Data	$F_{(2,20)} = 22.1$ $p < 0.001$	23	2.9 (0.5)	0.08 (0.02) 0.03 (0.09)	A-B temp B-C min	0.69
Summer (April-September)	$F_{(1,14)} = 49.4$ $p < 0.001$	16	-2.5 (1.3)	1.4 (0.2)	Log Area	0.78
Winter (October-March)	ns $p > 0.05$	-	-	-	-	-

Similar to that for herring, a model for quantifying ice consumption was developed and tested by partitioning the data into two groups. The groups were formed in the same manner as described previously. In this case, only one model was created, as no adequate predictions could be made from the data collected on odd-numbered Julian dates (Table 12). Even though the model itself accounted for a large proportion of the ice mass variance (93%), when tested, the predictions were unrelated to the actual quantity of ice consumed (Figure 12).

2.4 Discussion

The use of stomach temperature telemetry in captive harp seals has shown that the ingestion of fish and water (free and frozen) can be detected reliably (and see Gales and Renouf 1993). This study also found that the ingestion of ice and fish may be differentiated solely on the basis of stomach temperature parametres. However, contrary to Gales and Renouf (1993), the use of stomach temperature telemetry for quantifying prey consumption was not supported. Although statistically significant predictions of the quantity of herring consumed were possible (Table 5), the proportion of variance accounted for (27%) was low. Results pertaining to ice consumption were more promising, with the duration and magnitude of the temperature changes being related to the mass of ice consumed, accounting for 69% (Table 11) of the variance. However, further testing proved that this relationship was not robust.

The magnitude of the stomach temperature change may be a means to

Table 12

A model developed from a portion of the data set to predict the quantity of ice consumed by harp seals from known changes in stomach temperature. The model was subsequently tested using the remaining data.

Data used to create the model	n	Intercept (± SE)	Co-efficient (± SE)	Variable	r^2 and p level
Data gathered on even-numbered Julian days	12	-4.9 (±1.3)	-0.02 (±0.01) 2.0 (± 0.3)	B-C min Log Area	0.93 $p < 0.001$
Data gathered on odd-numbered Julian days	11	-	-	-	ns $p > 0.05$

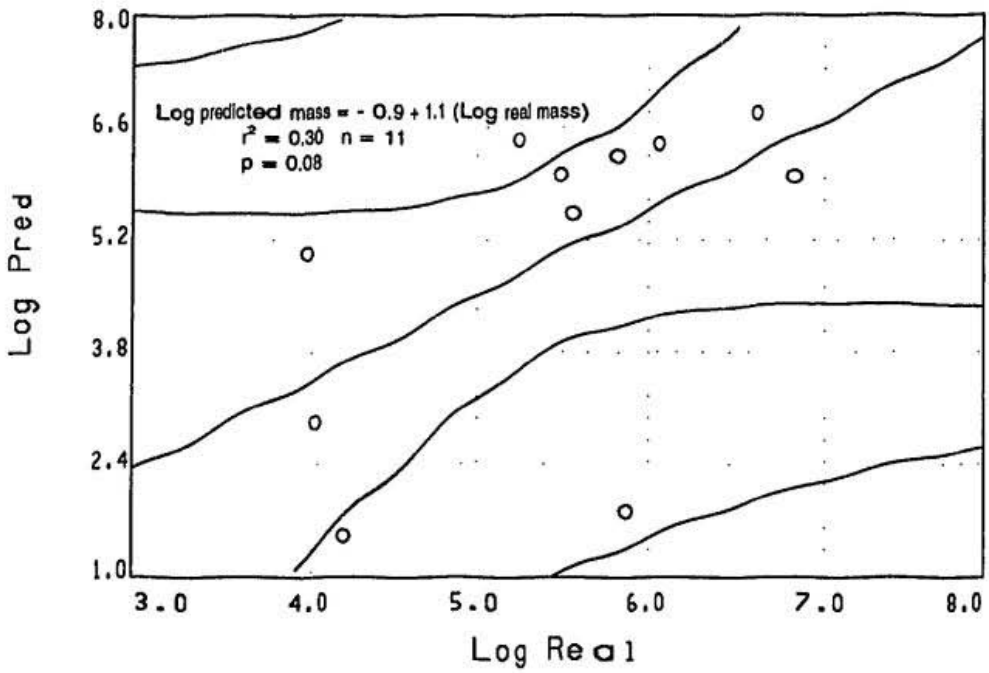


Figure 12: Predicted versus the actual mass of ice consumed by harp seals. The model was developed from data collected during even-numbered Julian days, and tested with data collected during odd-numbered Julian days. For model structure see Table 12.

indicate whether an ingested substance is a prey item or ice. When the seals consumed ice, the absolute change in stomach temperature was generally larger than when they ate fish. For example, when an adult female consumed 5430 grams of herring (mean T = -5.3 °C) stomach temperature dropped by only 6.5 °C. However, after consuming a similar amount of ice (5708 grams), a 32.2 °C drop in stomach temperature was recorded. Further, the smallest recorded meal of crushed ice (53 grams) resulted in a 16.6 °C change in stomach temperature, surpassing the maximum 15.4 °C temperature change resulting from a 3793 gram meal of fish (mean T = 0.3 °C).

Using 1 standard deviation as a criterion, these data suggest that rapid changes in stomach temperature which decrease by a minimum of 13.6 °C could likely be attributed to the ingestion of ice. Likewise, temperature changes of less than 7.8 °C could be attributed to fish consumption. With the present data set, using this criterion would result in 6 of 68 (8.8%) meals of herring and 5 of 27 (19.0%) meals of ice being misinterpreted. Feeding bouts resulting in temperature changes between 8 and 14 °C would have to be cautiously interpreted.

The magnitude and duration of stomach temperature change following a feeding bout depends upon the rate of heat flux from the body core to the stomach contents (Wilson and Culik 1991; Pütz and Bost 1994). Presumably, a number of factors influence this flux. The rate is dependent most simply upon the conductance of heat from the centre of the stomach to the stomach wall; this, in

turn, depending upon both the temperature gradient between the areas, and upon the thermal conductivity of the stomach contents (Wilson and Culik 1991). These factors coupled with differential digestive responses to various ingesta may help explain the dissimilarity in temperature profiles obtained from harp seals eating fish and ice.

When food is eaten by a seal it is transported almost immediately to the stomach, whereupon gastric juice secretion increases (Sanford 1992). The stomach's main functions in the digestive process are directly related to motility (Weisbrodt 1985); the musculature must first relax to accommodate the meal, and then contract to mix the ingested food with gastric juices, allowing digestion to begin. Finally, gastric motility is organized so as to propel the partially digested contents into the small bowel (Weisbrodt 1985). When the stomach becomes full peristaltic waves diminish in force, but subsequently increase in inverse proportion to the amount of fat in the meal (Davenport 1982). The rate of transfer of material from the stomach to the duodenum depends both upon the physical and chemical composition of the meal (Davenport 1978, 1982; Weisbrodt 1985). However, as a general rule, the greater the volume of gastric contents, the faster the rate of emptying (Sanford 1992). Liquids pass through the stomach more quickly than either solids or semi-solids (Davenport 1978), and the greater the concentration of energy (kcal/ml) in the gastric contents the lower the rate of transport to the duodenum (Davenport 1978; Hunt 1980). Hunt and Stubbs (1975) report that

when the stomach contains food, the rate of emptying is less than 10 ml/min, whereas the maximum rate of emptying for a stomach containing a saline solution is up to eight times faster.

The rate at which food heats up within the stomach depends partially upon the degree of mixing (Wilson and Culik 1991); high degrees of mixing result in the most rapid transfers of heat. When herring is eaten by a seal the rate of gastric mixing and emptying may be relatively slow. Both the high energy content of the food in general, and, not independently, because of its high fat content (Forbes and Swift 1944), herring may be expected to have a prolonged gut retention time. Given the slow rate of mixing, peripheral food could warm and subsequently insulate the body core from the remaining ingesta, which would warm more slowly (Wilson and Culik 1991). In contrast, when water or ice is ingested rigorous mixing of the fluids would inhibit the formation of a thermal gradient within the stomach (Wilson and Culik 1991), and ice would perhaps melt relatively quickly. It is also possible that upon melting some of the water may be lost through diffusion across the gastric wall. Considering the rapid rate at which liquids in general are emptied from the stomach (Davenport 1978), the potential loss of water across the gastric mucosa, and the lack of energy supplied to the seal by ingesting ice, the durations of stomach temperature change would perhaps be minimized, and their magnitudes maximized in comparison to those for meals of fish. The findings of this study were indeed consistent with these expectations (Tables 2 and 3). The

ability to distinguish between fish and ice consumption may become important when interpreting stomach temperature profiles from free-ranging animals.

The parametres which best predicted the mass of fish consumed by the seals were those measuring the duration of stomach temperature change following ingestion (log A-C min, log of B-C min) and the log of the area under the curve (Tables 4 and 5), however, these relationships were relatively weak. Partitioning the data by sex, season, and age of the subjects had little effect on the predicability of meal size (Table 5), but the number of subjects in each category was small (Table 1). Knowledge of the log of time elapsed from B-C accounted for 27% of the variability in the mass of herring fed to the seals. This amount increased to 80% when data for the juvenile animals were considered alone, but as in this case sample size was small (n = 7), no definitive conclusions should be drawn. The overall percentage of meal size variability accounted for in this study was substantially less than the 71% reported by Gales and Renouf (1993). This may perhaps reflect differences in the sample sizes used (n = 11 vs 68 in this study), and the deleterious effects of spurious correlations, or seasonal differences in metabolic rate (Renouf and Gales 1994). Data in this study were collected during a 15 month period, whereas those used by Gales and Renouf (1993) were collected during 4 months (September 1991 to January 1992). However, as the present data were partitioned and analyzed by season, this factor was unlikely to have seriously affected interpretation.

Testing the models created from sub-sets of the fish and ice consumption data (Tables 9 and 12) provided conflicting outcomes regarding the adequacy of the technique for quantifying rates of food and ice intake. The general trend being the smaller the sample size used to create the model, the higher the proportion of meal mass variance accounted for. The strongest relationships between stomach temperature parametres and meal mass were obtained with small sample sizes, both in this study and in Gales and Renouf (1993). This seems to indicate that the inherent variability in stomach temperature data becomes most evident with extensive sampling, and caution must be utilized when drawing conclusions based on limited sample sizes. It is recommended that large sample, species-specific calibrations be carried out before using this technique to estimate rates of food consumption.

One factor which seems particularly relevant for further determining the adequacy of stomach temperature probes in predicting the quantity of prey consumed by seals relates to an undetermined aspect of their foraging behaviour. Neither the temporal spacing, diurnal patterning nor the quantity of prey consumed during a meal is known for wild seals. In this study the majority of meals were large, with just 13 (19%) of the meals weighing less than 3 kg. This fact may prove problematic as it is unknown whether small and large sized meals can be detected equally well from changes in stomach temperature, and it is possible that this technique may prove most useful when larger discrete meals are eaten.

However, from Grémillet and Plös's (1994) study of the feeding ecology of free-living bank cormorants (Phalacrocorax neglectus), meals estimated to weigh as small as 6 g were readily identifiable from stomach temperature profiles. The adequacy of quantifying small versus large sized meals, or meals containing different sized prey item remains largely untested.

When Wilson et al. (1992) intubated African penguins with either 100 or 200 cm^3 of seawater, the integral of the temperature curve was less than expected. These results were explained on the basis that some of the seawater had been voided from the stomach before reaching asymptotic temperature, causing the smaller integral. It is possible that, with the large meals fed to captive seals in this study, some of the herring passed through to the intestine before being warmed to body temperature; resulting in an underestimate of the mass ingested. Support for this explanation comes from Markussen (1993), who estimated the time required for stomachs of harbour seals to empty. The stomachs of these seals, which were fed meals of herring ranging in mass from 0.5 to 2.1 kg, began to empty less than 1 hr after the end of feeding.

Further errors in this technique could result from the temperature sensors not being in continuous contact with incoming, colder prey items. Although the sensors were designed to sink in seawater (and in the stomach), we cannot say with any certainty where in the stomach they were positioned during the feeding experiments. Where multiple prey items were consumed during a meal, the

sensors may have been covered and consequently insulated from the temperature changes occuring as new prey items were eaten. Pütz and Bost (1994) note that stomach churning may potentially override this confound, but, as they conclude, its overall affect on temperature profiles or upon the adequacy of meal size prediction, is largely unknown.

Aside from differential digestive responses to various ingesta and potential errors in the technique outlined above, the nature of the feeding patter per se could obscure estimates of the quantity of prey consumed. The size and number of prey items taken in a meal as well as incidental water intake associated with different prey items could introduce error into meal size calculations. Consider differences in the water intake associated with meals consisting of limited numbers of large prey items, as opposed to those containing larger numbers of small fish, crustaceans, or cephalopods. Capturing numerous smaller prey items during a meal would presumably result in greater incidental water intake than would the capturing of larger prey items. Where seasonal and geographic differences in diet have been observed (Beck et al. 1993; Gales et al. 1993; Lawson et al. 1993), the accuracy of this technique may also be expected to shift accordingly. Within a particular species, these factors could combine to provide intake estimates couter to actual.

Despite the potential problems with quantifying prey consumption, combining the use of stomach temperature sensors with satellite telemetry and time-depth

recordings would provide valuable insight into the foraging ecology of seals. Information could be obtained on the timing and locations where seals feed, the temporal and geographic spacing of their meals, and the overall frequency of prey consumption. It would also be possible to determine if seals feed preferentially in certain portions of the water column and, as a result, may provide additional insight into the types of prey being consumed. Successful foraging dives could be readily identified as those containing rapid declines in stomach temperature. It would be interesting to compare success rates of dives with stomach temperature recorders to those which have traditionally been termed "foraging" and "non-foraging" dives based solely on the shape of the dive profile (Hindell et al. 1991; Le Boeuf et al. 1992).

That seals redistribute blood flow during diving, saving the oxygenated blood for the central nervous system and the heart (Schmidt-Nielsen 1983), may be problematic when interpreting profiles from free-ranging seals. Blood flow to the stomach would likely be reduced during dives, and rates of stomach perfusion and motility would perhaps be reduced (Pütz and Bost 1994). However, as these authors conclude, much of the heat flux to the stomach contents probably occurs as a result of conductance, irrespective of blood flow, and would therefore be unlikely to obscure interpretation of the data.

It is necessary to determine the distribution, diet and energy requirements of pinnipeds to evaluate their effects on commercial fisheries. Examining the hard

remains in stomach contents of seals have provided indication of both the type and the relative importance of particular prey items to the diet. However, differential degradation and passage rates of different prey types bias estimates of consumption based on this method (Pierce and Boyle 1991). For example, the percentage of otoliths fed to phocid seals which were subsequently recovered in stomach contents dropped from 100 to 0% between 0 and 12.9 hours following ingestion (Murie and Lavigne 1986). Thus, the estimated relative importance of different fish species in the diet may be incorrect when using solely otolith remains. Alternately, the accumulation of cephalopod beaks in seal stomachs may over-estimate the importance of these items to the diet (Bigg and Fawcett 1985). The extent of tissue and hard part erosion increases with time elapsed since feeding, and would be most deleterious for prey which contain no hard remains.

For harp seals, quantitative descriptions of diet are further complicated by seasonal and geographic changes in population distribution; animals are most accessible for sampling during the brief lactation and moulting periods. The diet of harp seals from the Gulf of St. Lawrence and Western Hudson Straight has been shown to vary seasonally (Beck et al. 1993). Further, considerable seasonal, geographic and interannual variation in the diet of harp seals in the Newfoundland and Labrador region has been found (Lawson et al. 1993). These studies demonstrate the necessity of using extended temporal and geographic sampling regimes when estimating the impact of migratory seals on commercial fish stocks.

Food intake has also been estimated indirectly by measuring labelled-water dilution rates. Such consumption estimates require knowledge of metabolic water production, prey composition and metabolic efficiency (Costa 1987). Animals must be injected and recaptured within a few days, which is possible only during lactation and moult for most wild seals. Consumption estimates obtained in this manner would be inappropriate for estimating annual rates of food consumption for either harbour or harp seals, as the energy requirements of these animals vary substantially over the year (Renouf and Noseworthy 1991; Renouf et al. 1993). Energy requirements of seals have also been estimated from serial changes in mass (Fedak and Anderson 1987). Again, this method would be inappropriate for harbour and harp seals, as the relationship between energy intake and body mass is not constant throughout the year (Renouf and Noseworthy 1991; Renouf et al. 1993). Finally, data obtained from long-term studies of the energy requirements of captive seals may be used to estimate the food requirements of wild populations. Such studies can provide details into particular aspects of the energy budget such as basal energy requirements, digestive efficiencies and the costs of swimming and digestion. If activity budgets are known for free-ranging individuals, data obtained from captive animals might be scaled to estimate the energy requirements of their wild counterparts. It seems clear that in order to obtain reasonable estimates of the type and rate of prey consumed by seals that a comprehensive approach involving a variety of research methods is necessary.

3.0 Chapter 3

Use of Temperature Telemetry to Monitor Ingestion by a Harbour Seal (Phoca vitulina) Mother and her Pup Throughout Lactation

3.1 Introduction

Relatively little is known about the characteristics of pinniped suckling behaviour despite its importance to the understanding of lactation strategies. Bowen (1991) noted the difficulty in accurately measuring nursing events such as bout duration, inter-suckling interval and daily suckling duration per se, along with ontogenetic variation in these parametres. Where estimates exist, comparisons between studies are often difficult as definitions of suckling bout parametres and methods of measurement are variable (Bowen 1991; Perry and Stenson 1992).

Existing data on suckling behaviour have largely relied on visual observations. As such, they are typically restricted to daylight hours and to animals within close proximity to the observer. Estimates of total daily suckling duration are usually based on the assumption that bout lengths measured during the day are representative of the entire 24 h period, even though diel variations have been reported (Limberger et al. 1986). These uncertainties may be compounded if the pattern of suckling changes over the lactation period. An increase in the duration of suckling sessions with pup age has been reported for northern and southern elephant seals (Mirounga spp., Bowen 1991), as well as for harbour seals (Rosen 1991).

Two methods have generally been used to quantify milk intake by pinnipeds (Costa 1991). The first calculates the amount of milk necessary to meet a pup's estimated energy metabolism and growth during lactation (Fedak and Anderson 1982; 1987). The second estimates milk intake by monitoring the decline of the specific activity or concentration of introduced labelled-water (Costa et al. 1986; Oftedal and Iverson 1987; Tedman and Green 1987; Higgins et al. 1988; Costa 1991; Lydersen et al. 1992). In both methods, a cumulative estimate of milk intake is obtained which provides no information on the variance of daily or diurnal suckling patterns. Knowledge of ontogenetic and temporal shifts in suckling behaviour would compliment information provided by purely energetics research.

The development of archival units capable of detecting and recording changes in stomach temperature have widened the scope of feeding research in marine endotherms (see Chapter 1). The present study used stomach temperature probes to monitor ingestion by a female harbour seal and her nursing pup. Due to its preliminary nature, and small sample size, the main purpose of the study was to investigate the potential use of the stomach temperature technique per se in this situation. Therefore, the most basic objective was to determine if nursing bouts could be identified from changes in pup stomach temperature, and if so, to determine whether a relationship existed between the duration of a suckling session and the subsequent length of stomach temperature change. The possibility of being able to remotely detect milk intake, and thereby providing a

means through which to investigate ontogenetic changes in suckling behaviour could be were also investigated.

3.2 Methods and Materials

A 15-year-old harbour seal and her female pup born on 24 June, 1992 at the Ocean Sciences Centre, Memorial University of Newfoundland, Canada were studied. The seals were housed in an outdoor tank (7.5 m diametre) surrounded by wooden decking. The tank was filled with 60,000 litres of seawater at ambient temperature (mean temperature during the study =9.2 °C, range=7.5°C to 13.0 °C) pumped continuously from the adjacent Logy Bay. The mother was fed pre-weighed thawed herring (Clupea harengus) ad libitum for 30 minutes each morning, and the mass of food she consumed each day was recorded. Both mother and pup were weighed at least weekly using a platform suspended under a Salter model 199 Thermoscale. Six days after birth, the pup was induced to swallow a temperature-sensitive VHF transmitter (Biotrack, Dorset, UK) which she retained throughout the lactation period. The mother was also given a similar temperature transmitter, placed in a fish, on three consecutive occasions which she retained for periods ranging from 1 to 9 days.

The temperature-sensitive VHF transmitters were housed in watertight plastic cylinders (51.3 mm in height, 17.7 mm diameter, 11 g). Pulse duration was received with a 2-element Yagi antenna and logged by a Lotek receiver (SRX 400;

Lotek Engineering Inc., Aurora, Ont., Can.). Calibrations were performed in a waterbath prior to the experiment, where sensors were maintained for 15 minutes at each 5 °C interval between 0 and 40 °C. Transmitters responded to temperature changes within 1 minute, and were precise to within ± 0.2 °C of the waterbath temperature. Curve-fitted polynomial equations were used to calculate stomach temperature from logged pulse durations.

Visual observations of the pair were conducted between 0900 and 1600 h each day. Records were kept of the beginning and end of each suckling session, as well as all on- and off-teat times. The duration of any one suckling bout was calculated as the cumulative amount of time the pup was attached to the teat, provided that intermittent off-teat periods did not exceed 1 consecutive minute in duration. When the pup had been unattached to the nipple for more than 1 minute, any subsequent nursing was recorded as a new bout.

To estimate the amount of milk ingested, the pup's stomach was simulated in the laboratory using an empty balloon that could be filled with milk, following the method of Wilson et al. (1992). The balloon was immersed in a 4 litre waterbath set at the pup's mean stomach temperature (37.8 °C). Temperature changes similar to those of the nursing pup were brought about by introducing various quantities of low-fat cow's milk or cream, as an instantaneous volume, into the balloon. The milk or cream was introduced at 37.1 °C, a temperature which was within 1 SD of mother's mean body temperature of 37.5 °C. To account for the

possible affect of changes in milk composition throughout the lactation period, simulations were run using milk/cream with two different percentages of fat (2% milk fat n=13; 32% milk fat n=4). Temperature changes in the simulated stomach were monitored with a VHF transmitter. From these trials a relationship was determined between the volume of milk added to the balloon and the length of time required for the introduced milk to warm to the bath temperature. Similar to calibration results in Chapter 2, both classic and inverse linear regressions of these data were provided.

Pup stomach temperature change following nursing was analyzed relative to two operationally defined points: (A) the time of departure from stable temperature, and (C) the time at which a stable temperature (within ± 0.1 °C) of (A) was obtained subsequent to the nursing bout. Observed nursing bouts precipitated measured stomach temperature drops followed by exponential or linear returns to stable values. Nursing bouts which were inferred from the temperature records followed an exponential recovery ($Y=A(1-e^{-B(X-C)}$; where X=time, Y=temperature, and A,B,C are parametres estimated by the mathematical model) in order to provide agreement between this and previously published work (Wilson et al 1992, 1993; Weimerskirch and Wilson 1992). To reduce bias in deciding which of the unobserved temperature changes were indicative of nursing activity, only those instances for which the preceding equation accounted for greater than 90% of the variance in temperatures were included in the following

analyses. Using 90% as the cut-off criterion resulted in just 5 of the 58 (8.6%) potential nursing bouts being discarded. In much of the discarded data, stomach temperatures followed a linear, as opposed to an exponential, return to stable value.

All data were analyzed using the Number Cruncher Statistical System (NCSS, Kaysville, Utah) software version 5.03 and the Curve Fitter program version 5.9. In all cases, probability levels of less than 5% were accepted as statistically significant.

3.3 Results

The pup weighed 11 kg at birth. During the first 27 days of lactation its mass increased to 27.5 kg (Figure 13). The mother's mass declined by 24.6%, to a low of 65 kg (Figure 14), although the amount of food she consumed per day increased during the same period (one-way ANOVA for mean food intake across weeks; $F_{(4,30)}=24.29$, $p < 0.0001$).

The mother-pup pair was observed for a total of 83.5 hours, and 131.0 and 457.5 hours of stomach temperature data were recorded from the mother and pup, respectively, between 30 June and 31 July, 1992. On 17 occasions, temperature profiles indicating nursing were matched by visual observation. Suckling bouts were inferred from another 53 temperature profiles without visual confirmation. Figure 15 provides an example of a daily temperature profile obtained from the

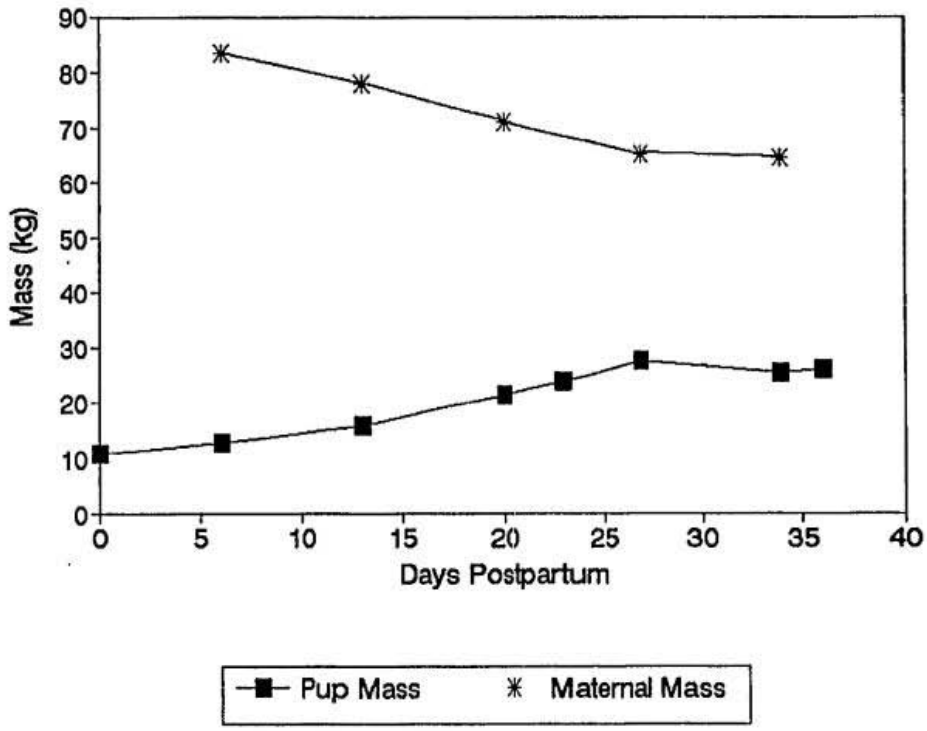


Figure 13: Changes in total body mass of a harbour seal mother and pup from 0 to 36 days postpartum.

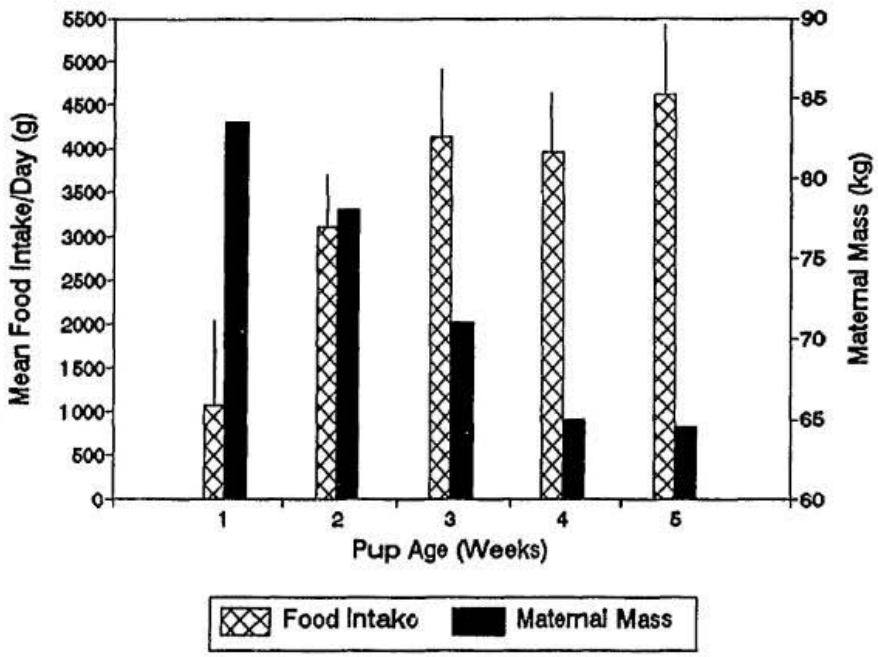


Figure 14: Mean daily food intake (g of herring) during the lactation period, with reference to decreasing maternal mass (kg). Vertical lines represent 1 standard deviation.

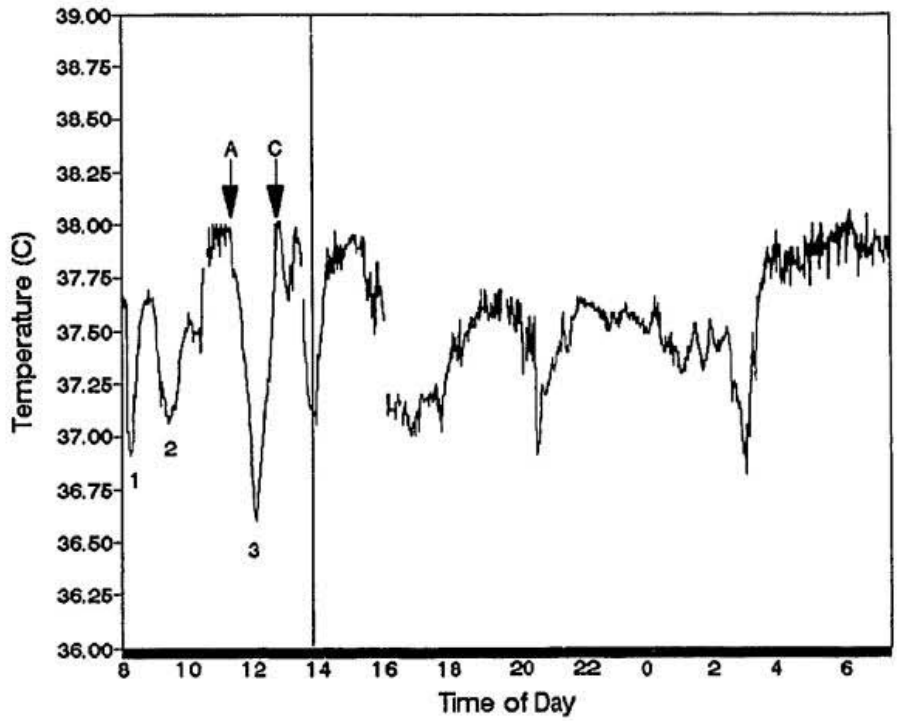


Figure 15: Daily stomach temperature profile of a suckling harbour seal pup, obtained at 8 days of age. Arrows indicate the beginning and end of stomach temperature change following milk intake (A and C). The vertical line indicates the time when observations ended for that day. Stomach temperature changes marked 1-3 correspond with observed nursing bouts.

nursing pup. Temperature changes such as those occurring between the arrows in Figure 15 followed observed nursing sessions. The length of stomach temperature change (A to C in minutes) following milk intake was linearly related to the duration of the nursing bout (Figure 16; r^2=0.82, $p < 0.001$, n = 17).

In addition, 9 instances of nursing or nursing attempts were observed while the pair were in the water; none of these nursing attempts coincided with decreases in stomach temperature. However, in 5 of these 9 instances the pair hauled out of the water and nursed, on average, 11.6 ± 6.9 minutes after the attempt had been observed. The overall non-feeding stomach temperatures of mother and pup fell within the range of published values for mammals (Schmidt-Nielsen 1983), and varied between 37.1-38.2 °C and 37.2-38.5 °C for mother and pup, respectively. All telemetry analyses were of data collected between 1-28 July, 1992, and divided into 4 week-long blocks. It was during this time period that sampling protocol by observers and the use of telemetry equipment was most constant.

The introduction of milk or cream into the simulated stomach resulted in temperature decreases (Figure 17). As no differences in recovery time were found between simulations using substances with high and low percentages of fat (one-way ANOVA; $F_{(1,6)}$=0.11, $p > 0.05$), all data were analyzed together. The time elapsed from temperature decrease to stable temperature recovery during the simulation trials was significantly related to the volume of milk introduced into the

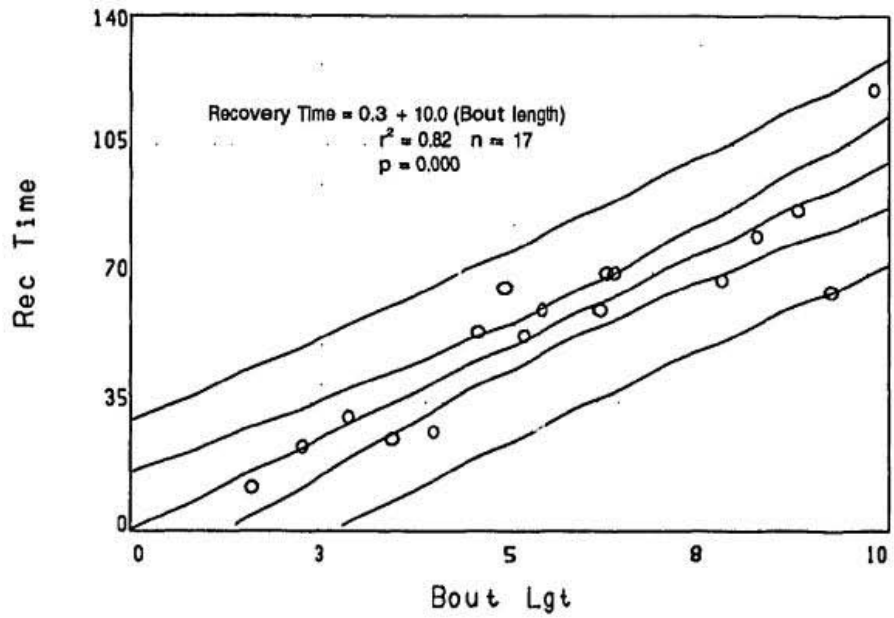


Figure 16: Relationship between the duration of stomach temperature change (recovery time) and nursing bout length.

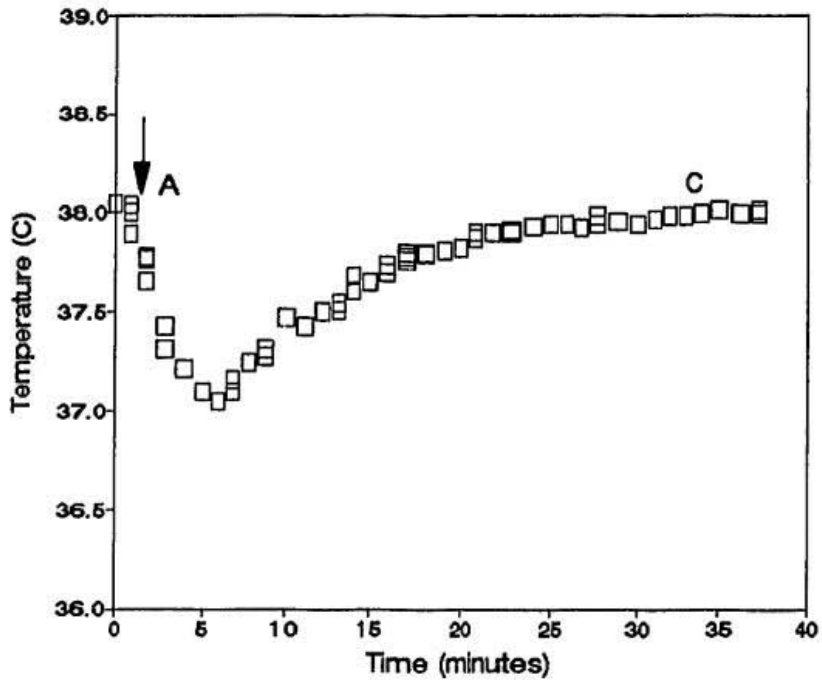


Figure 17: Typical temperature changes, recorded via telemetry, in a milk-filled balloon during stomach simulations. In this case 375 ml of milk at 37.1 C was added to the balloon, at the time indicated by the arrow. The points A and C are also shown.

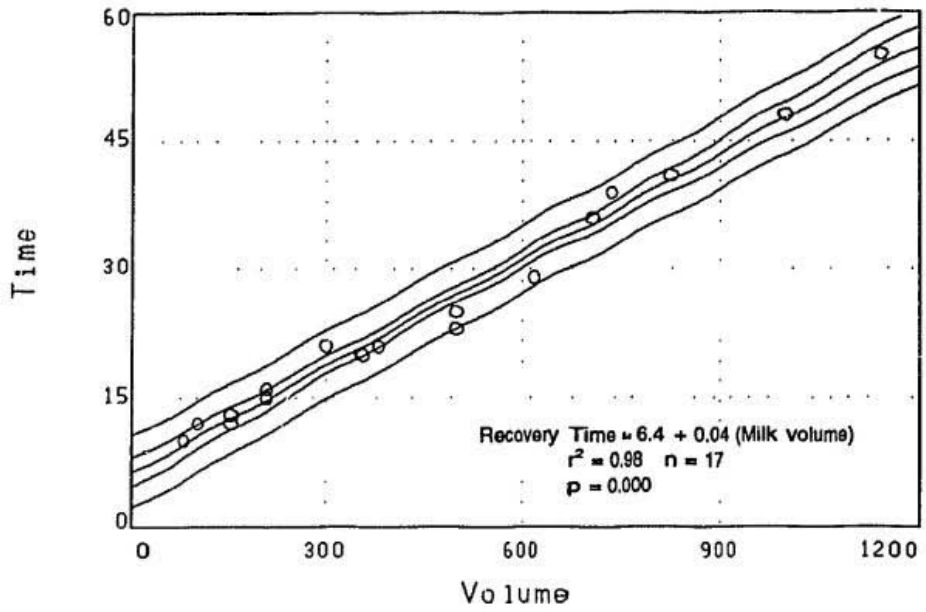
balloon (Figure 18; r^2=0.98, $p < 0.001$, n=17). There was no difference between the classic and inverse methods with respect to either the proportion of variance accounted for or the significance level of the data. The estimate of errors for the predicted values were also similar.

Extrapolating from these simulation experiments, the duration of stomach temperature change was used to estimate the volume of milk ingested by the pup. The time elapsed from onset of post-prandial temperature drop to stable temperature recovery increased with pup age, as did the estimated milk intake per bout (Table 13; one-way ANOVA; $F_{(3,67)}$=11.66, $p < 0.0001$ for both data sets). Specifically, the duration of stomach temperature change following nursing bouts was significantly lower in week 1 than subsequently (Fisher's LSD test, $p < 0.01$).

A shift towards diurnal nursing time was evident across weeks, with an overall increase in milk intake during the hours of 06:00 to 18:00 (Figure 19; Kruskal-Wallis one-way ANOVA; H=9.76, df=3, $p < 0.05$). The percentage of nursing which occurred during the day in week 4 was significantly greater than in week 1 (Dunn's multiple comparison test, $p < 0.05$). This trend was evident when the length of stomach temperature change (A to C) was considered as a percentage of the total for a given day, independent of the actual number of nursing sessions.

Figure 20 provides an example of stomach temperature data collected from the mother. The rapid drops in temperature evident in this graph can only be

a.



b.

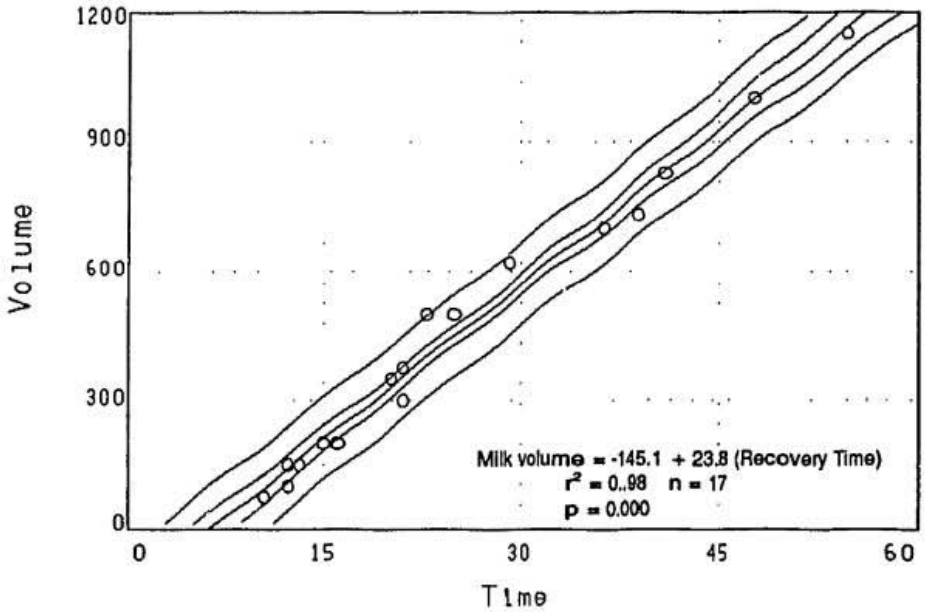


Figure 18: a) Classic and b) Inverse regressions of the relationship between the volume of milk added to a simulated stomach and the time required for the introduced milk to warm to the bath temperature. Confidence intervals as in Figures 4-6.

Table 13

Changes over the lactation period in the total length of stomach temperature change (A-C minutes) following milk ingestion, and the estimated amount of milk consumed (millilitres). Post hoc comparisons were performed with Fisher's LSD procedure, with indicated differences being significant at the 0.05 probability level ($a \neq b$; $c \neq d$).

Time	Pup Age (Weeks)	n	Duration of Temperature Change (A-C min) Mean	SD	Estimated Milk Intake per Bout (ml) Mean	SD
Week 1	1-2	21	26.6^{a}	10.5	488.1^{c}	250.7
Week 2	2-3	23	48.9^{b}	19.0	1019.6^{d}	454.0
Week 3	3-4	9	52.4^{b}	18.6	1104.7^{d}	442.8
Week 4	4-5	18	56.9^{b}	20.5	1210.5^{d}	489.6

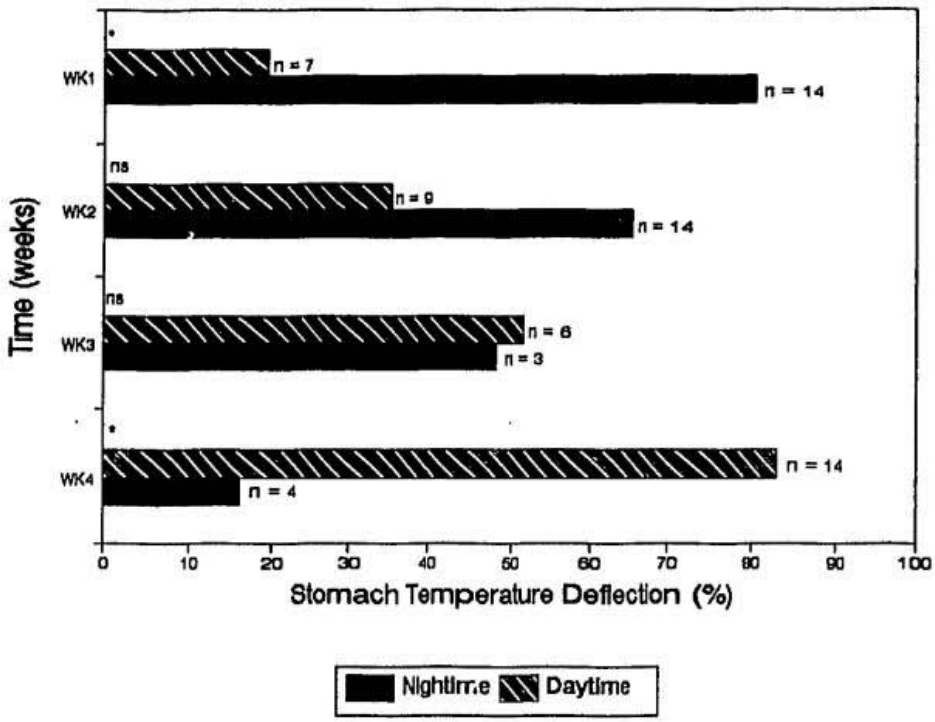


Figure 19: Percentage of total stomach temperature change occurring during the day and night (06:00 to 18:00 and 18:00 to 06:00, respectively) using the duration of temperature change (time from A to C) as the criterion.

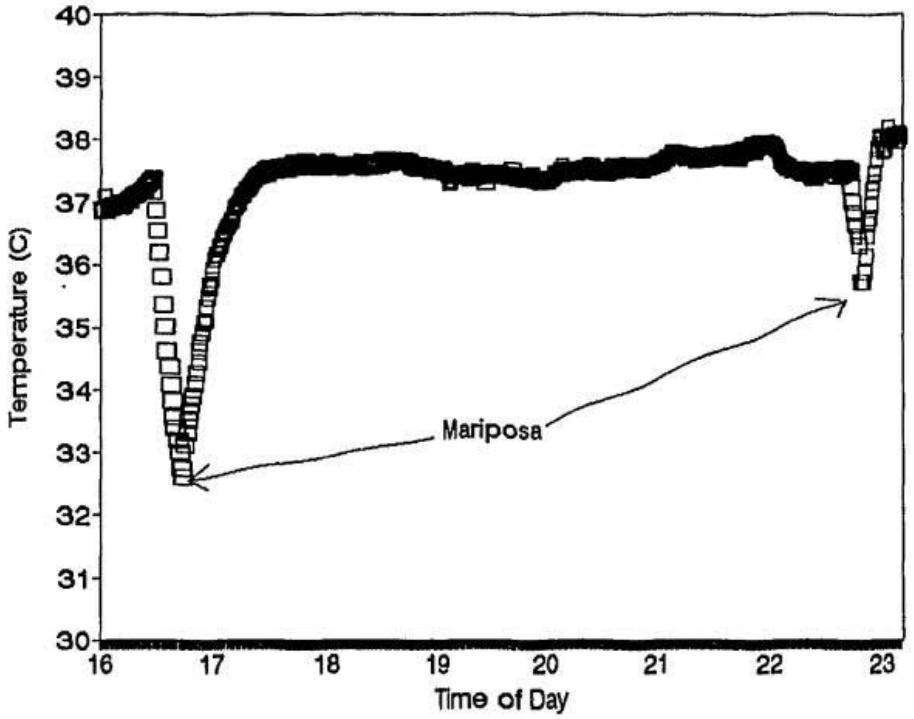


Figure 20: Apparent mariposa (seawater drinking) in the stomach temperature profile of a lactating harbour seal. Temperature was logged continually while the animal had access only to ambient temperature seawater.

attributed to seawater drinking (mariposa) as the weather conditions and daily feeding regime precluded the possibility of fresh water, ice, snow, or food intake at these times.

3.4 Discussion

Temperature telemetry may prove to be useful as a tool for directly monitoring milk intake in harbour seals. Unlike labelled-water techniques and calculation of energy requirements during lactation, stomach temperature telemetry provides detailed data which can be partitioned over time. Such a tool, if applied successfully to free-ranging seals, could provide a valuable means through which to investigate pinniped lactation strategies and maternal investment. For example, differential maternal investment by pup sex could be comparatively addressed, as could the attendance patterns of mothers of different age and with differing levels of experience.

Although obtained in a captive situation, the mass changes exhibited by the mother and her pup are similar to those reported for free-living harbour seals (Boulva and McLaren 1979; Rosen 1991; Bowen et al. 1992). The lactation period of 36 days falls within the range of published values (23-43 days; Bowen, 1991), as does the 2.5-fold mass increase of the pup (Bowen et al. 1992). Maternal mass loss was somewhat less than that reported for free-ranging females since the mother in this study was fed (Bowen et al. 1992). However, that the female

still exhibited a 24% decrease in body mass from parturition to weaning despite ad libitum feeding indicates the extent of reserve depletion during lactation.

The inferred increase in suckling bout length with pup age in this study (Figure 16 and Table 13) is similar to that seen in wild harbour seal pups on the western Atlantic island of Miquelon (Rosen 1991). However, as the present study estimates the volume of milk ingested per bout, it is unknown whether the total amount ingested per day changed with pup age. Oftedal et al. (1991) reported that milk intake was unaffected by lactation stage in harbour seals on Sable Island, with equal intake occurring in early (8-12 days) and late lactation (19-22 days).

The pup's changing nursing regime from largely nocturnal to daytime during the study provides data that would be missed using a purely observational approach. These data, coupled with observations of maternal mariposa (seawater drinking), are interesting findings.

Documentation of free-water ingestion is critical to isotopic studies of food consumption and energetics which assume all water intake to be bound within the prey or milk (Nagy and Costa 1980). This assumption is invalid in harbour seals (present study), harp seals (Renouf et al. 1990; Gales and Renouf 1993), ringed seals (Phoca hispida; Lydersen et al. 1992), grey seals (Halichoerus grypus; Schweigert 1993) and Weddell seals (Leptonchytes weddellii; Tedman and Green 1987). Such mariposa would lead to overestimates of prey consumption by pinnipeds.

. The overall importance of mariposa, snow and ice consumption to maintaining water balance in pinnipeds is not fully understood. Lydersen et al. (1992) suggested that snow consumption by a nursing ringed seal pup may have been influenced by the length of time since the pup consumed its last meal. It seems possible that this explanation may be more generally applicable. When feeding occurs frequently, pinnipeds may obtain sufficient amounts of water from their food, and alternative sources may not be required. However, when fasting, or when access to food is limited, animals may compensate by actively consuming seawater, ice or snow. Support for this view is available from harp seals (Renouf et al. 1990), where daily fresh water and fish consumption were negatively related.

In the present study, no attempt was made to measure the temperature of the milk as it came from the mother. Presumably, milk temperature would vary with activity level and with variance in the mother's body temperature. It would be desirable to quantify this variable in future studies. As noted by Wilson et al. (1992), who conceived using stomach simulations to estimate prey consumption by free-ranging birds, direct feeding experiments using ingesta of known temperature and volume would improve the accuracy of such indirect estimates. Likewise, direct pup feeding experiments using known quantities of mother's milk would be required to determine the accuracy of the indirect intake estimates in the present study.

While it offered a simplified physical model, many inherent limitations were

apparent when using the balloon method to estimate milk intake by the seal pup. The balloon is essentially a closed system, and is deficient at modelling the many digestive processes which occurred in the stomach (see Chapter 2). For example, the balloon model did not account for changes in temperature which may have occurred as the milk mixed with either prior gastric contents or from the influx of secretions as milk reached the stomach. Perhaps most fundamentally, however, the model did not account for gastric motility. Considering its nature, milk would likely be well mixed within the stomach, would warm rapidly, and would have a relatively short gut retention time. Also, as the balloon was in essence closed, it did not account for losses which occurred as milk passed on to the duodenum, or as water diffused through the gastric wall. From this standpoint, the balloon model perhaps overestimated the volume of milk ingested by the pup.

The duration of temperature change following nursing is affected by the temperature and volume of milk ingested, the temperature difference between the milk and the seal, as well as the many processes of digestion. Presumably, the overall temperature change resulting from the addition of large volumes of milk into an empty balloon would be greater than that which would occur in the stomach of a nursing pup. However, in this study, milk temperature (estimated from the mother's body temperature) was not related to the subsequent duration of stomach temperature change (r^2=0.13, p=0.28, n=11).

Stomach temperature telemetry, using the archival units described by

Wilson et al. (1992), would be a useful tool for estimating maternal prey consumption and mariposa during lactation. These measures and methodological improvements would help refine estimates of mass and energy transfer for harbour seals and other species which are known to feed during lactation (Boness et al. 1993; Lydersen and Kovacs 1993).

4.0 Chapter 4

General Discussion

Results of the present research with captive seals indicate that the use of stomach temperature probes may provide a valuable tool for remotely monitoring ingestion by free-ranging phocid seals. Chapter 2 explored the efficacy of using stomach temperature probes to quantify harp seal feeding behaviour. Although this use of the technique was not supported, the ingestion of both fish and ice could be reliably detected (and see Gales and Renouf 1993). In addition, results indicated that the magnitude of the decrease in stomach temperature may indicate whether the ingested substance was a prey item or ice.

In Chapter 3, data were reported from a harbour seal mother and pup fitted with stomach temperature probes throughout the lactation period. Monitoring the stomach temperature changes of nursing pups may provide a novel and relatively nondisruptive method for both detecting and estimating the approximate volume of milk consumed per nursing bout, as well as provide a useful means through which the temporal aspects of nursing may be resolved. Once reasonably tested, this technique may provide an advantage over behavioural observation alone, in that continuous 24 hr records of nursing activity could be recorded.

An equally interesting application of this technique throughout the nursing period could come from its use with the lactating females. Recently, diving records from lactating harbour (Boness et al. 1993) and harp seals (Lydersen and Kovacs

1993) suggest that these species may forage throughout the lactation period. Boness et al. (1993) speculate that many of the smaller phocid seals may feed extensively during lactation to support maintenance and growth of their pups. This is in contrast to the belief held previously that most female phocid seals fast during lactation (Bonner 1984; Costa 1991; Boness et al. 1993; Lydersen and Kovacs 1993). Indeed, fasting as opposed to temporally dispersed foraging and attendance cycles is cited as one of the major differences in the maternal strategies of phocids and otariids. Deploying stomach temperature probes in conjunction with time-depth recorders on other species of lactating females may reveal the true extent of this phocid/otariid difference.

It is plausible that stomach temperature telemetry in conjunction with satellite-linked time-depth recorders[1] will become a widely-used technique for investigating the foraging ecology and energetics of free-ranging pinnipeds, as it has to investigate aspects of the foraging behaviour of free-living wandering albatrosses (Weimerskirch et al. 1994). During the incubation and brooding periods, the foraging ranges and success rates of wandering albatrosses were recorded. Data indicated that albatrosses foraged on widely dispersed prey items which were encountered, on average, every 4.4 hours during daylight periods, and it was estimated that they ingested 2.1 kg of prey per day. Although it seems

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R. Hill (Wildlife Computers) is currently developing single-package satellite-linked stomach temperature recorders which will enable direct detection of food consumption in free-living seals.

likely that prey ingestion could be detected using this technique in many species, this thesis has demonstrated the necessity of performing large sample-sized, species-specific calibrations prior to using the technique to estimate rates of prey consumption. Different sizes and types of prey, as well as differences in body temperature, stomach, and, indeed, total body size could potentially affect the accuracy of equations predicting the mass of prey ingested.

Literature Cited

Amos W, Twiss S, Pomeroy PP, Anderson SS (1993) Male mating success and paternity in the grey seal, Halichoerus grypus: A study using DNA fingerprinting. Proc R Soc Lond B 252:199-207

Beck GG, Hammill MO, Smith TG (1993) Seasonal variation in the diet of harp seals (Phoca groenlandica) from the Gulf of St. Lawrence and the Western Hudson Straight. Can J Fish Aquat Sci 50:1363-1371

Bigg MA, Fawcett I (1985) Two biases in diet determination of northern fur seals (Callorhinus ursinus). In Beddington JR, Beverton RJH, Lavigne DM (Eds) Marine Mammals and Fisheries, George Allen and Unwin Press, London, pp 284-291

Boness DJ, Bowen WD, Oftedal OT (1993) Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seal. Behav Ecol Sociobiol 34:95-104

Bonner WN (1984) Lactation strategies in pinnipeds: Problems for a marine mammalian group. Symp zool Soc Lond 51:253-272

Boulva J, McLaren IA (1979) Biology of the harbor seal, Phoca vitulina, in eastern Canada. Bull Fish Res Board Can 200:1-24

Bowen WD (1991) Behavioural ecology of pinniped neonates. In: Renouf D (Ed) Behaviour of Pinnipeds, Chapman and Hall, New York, pp 66-117

Bowen WD, Oftedal OT, Boness DJ (1992) Mass and energy transfer during lactation in a small phocid, the harbor seal (Phoca vitulina). Physiol Zool 65:844-866

Boyd I, Arnbom T, Fedak M (1993) Water flux, body composition, and metabolic rate during molt in female southern elephant seals. Physiol Zool 66:43-60

Costa DP (1987) Methods for studying the energetics of freely diving mammals. Can J Zool 66:45-52

Costa DP (1991) Physiology of behaviour in pinnipeds. In: Renouf D (Ed) Behaviour of Pinnipeds, Chapman and Hall, New York, pp 236-286

Costa DP, Le Boeuf BJ, Huntley AC, Oritz CL (1986) The energetics of lactation in the northern elephant seal, Mirounga angustirostris. J Zool, Lond 209:21-

33

Davenport HW (1978) A Digest of Digestion. Year Book Medical Publishers, Inc., Chicago, Ill, USA

Davenport HW (1982) Physiology of the Digestive Tract. Year Book Medical Publishers, Inc., Chicago, Ill, USA

Fedak MA, Anderson SS (1982) The energetics of lactation: Accurate measurements from a large wild mammal, the Grey seal (Halichoerus grypus). J Zool, Lond 198: 473-479

Fedak MA, Anderson SA (1987) Estimating the energy requirements of seals from weight changes. In Huntley AC, Costa DP, Worthy GAJ, Castellini MA (Eds) Approaches to Marine Mammal Energetics, Allen Press, Lawrence, KS, pp 205-223

Forbes EB, Swift RW (1944) Associative dynamic effects of protein, carbohydrate and fat. J Nutr 27: 453-468

Gales R, Renouf D (1993) Detecting and measuring food and water intake in

captive seals using temperature telemetry. J Wildl Manage 57:514-519

Gales R, Pemberton D, Lu CC, Clarke MR (1993) Cephalopod diet of the Australian fur seal: Variation due to location, season and sample type. Aust J Mar Freshwater Res 44:657-671

Grémillet DJH, Plös AL (1994) The use of stomach temperature recorders for the calculation of daily food intake in cormorants. J exp Biol 189:105-115

Harwood J, Croxall JP (1988) The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. Mar Mamm Sci 4:13-33

Higgins LV, Costa DP, Huntley AC, Le Boeuf BJ (1988) Behavioral and physiological measurements of maternal investment in the Stellar sea lion, Eumetopias jubatus. Mar Mamm Sci 4:44-58

Hindell MA, Slip DJ, Burton HR (1991) The diving behaviour of adult male and female southern elephant seals, Mirounga leonina (Pinnipedia: Phocidae). Aust J Zool 39:595-619

Hunt JN (1980) A possible relation between the regulation of gastric emptying and food intake. Am J Physiol 239:G1-G4

Hunt JN, Stubbs DF (1975) The volume and energy content of meals as determinants of gastric emptying. J Physiol London 245:209-225

Kovacs K (1987a) Maternal behaviour and early behavioural ontogeny of grey seals (Halichoerus grypus) on the Isle of May, UK. J Zool,Lond 213:697-715

Kovacs, K (1987b) Maternal behaviour and early behavioural ontogeny of harp seals, Phoca groenlandica. Anim Behav 35:844-855

Kovacs K, Lavigne DM (1992) Maternal investment in otariid seals and walruses. Can J Zool 70:1953-1964

Krutchkoff RG (1967) Classical and inverse regression methods of calibration. Technometrics 9:425-439

Lawson JW, Renouf D (1985) Parturition in the Atlantic harbour seal, Phoca vitulina concolor. J Mammal 66:395-398

Lawson JW, Renouf D (1987) Bonding and weaning in harbour seals, Phoca vitulina. J Mammal 68:445-449

Lawson JW, Stenson GB, McKinnon DG (1993) Diet of harp seals (Phoca groenlandica) in 2J3KL during 1991-93. NAFO SCR Doc 93/36 15 pp

Le Boeuf BJ (1986) Sexual strategies of seals and walruses. New Scient Jan:36-39

Le Boeuf BJ, Costa DP, Huntley AC, Feldkamp SD (1988) Continuous, deep diving in female northern elephant seals, Mirounga angustirostris. Can J Zool 66:446-458

Le Boeuf BJ, Naito Y, Asaga T, Crocker D, Costa DP (1992) Swim speed in a female northern elephant seal: Metabolic and foraging implications. Can J Zool 70:786-795

Limberger D, Trillmich F, Biebach H, Stevenson RD (1986) Temperature regulation and microhabitat choice by free-ranging Galapagos fur seal pups (Arctocephalus galapagoensis). Oecologia 69:53-59

Lydersen C, Hammill MO, Ryg MS (1992) Water flux and mass gain during lactation in free-living ringed seal (Phoca hispida) pups. J Zool, Lond 228:361-369

Lydersen C, Kovacs KM (1993) Diving behaviour of lactating harp seal, Phoca groenlandica, females from the Gulf of St. Lawrence, Canada. Anim Behav 46:1213-1221

Markussen NH (1993) Transit time of digesta in captive harbour seals (Phoca vitulina). Can J Zool 71:1071-1073

Martinelle S (1970) On the choice of regression in linear calibration. Comments on a paper by RG Krutchkoff. Technometrics 12:157-161

McCann TS (1980) Territoriality and breeding behaviour of adult male Antarctic fur seal, Arctocephalus gazella. J Zool, Lond 192:295-310

Murie DJ, Lavigne DM (1986) Interpretation of otoliths in stomach content analyses of phocid seals: Quantifying fish consumption. Can J Zool 64:1152-1157

Nagy KA, Costa DP (1980) Water flux in animals: Analysis of the potential errors

in the tritiated water method. Am J Physiol 238:R454-R465

Oftedal OJ, Bowen WD, Boness DJ (1991) Lactation performance is unaffected by lactation stage in harbor seals (Phoca vitulina) on Sable Island. Ninth Biennial Conference on the Biology of Marine Mammals Chicago, Ill (Abst)

Oftedal OJ, Bowen WD, Boness DJ (1993) Energy transfer by lactating hooded seals and nutrient deposition in their pups during the four days from birth to weaning. Physiol Zool 66:412-436

Oftedal OJ, Iverson SJ (1987) Hydrogen isotope methodology for measurement of milk intake and energetics of growth in suckling young. In: Huntley AC, Costa DP, Worthy GAJ, Castellini MA (Eds) Approaches to Marine Mammal Energetics, Allen Press, Lawrence, KS pp 67-96.

Perry EA, Stenson GB (1992) Observations on nursing behaviour of hooded seals, Cystophora cristata. Behaviour 122:1-10

Pierce GJ, Boyle PR (1991) A review of the methods for diet analysis in piscivorous marine mammals. Oceanogr Mar Biol Annu Rev 29:409-486

Pütz K, Bost CA (1994) Feeding behavior of free-ranging King penguins (Aptenodytes patagonicus). Ecology 75:489-497

Renouf D, Gales R (1994) Seasonal variation in the metabolic rate of harp seals: Unexpected energetic economy in the cold ocean. Can J Zool 72:1625-1632

Renouf D, Gales R, Noseworthy E (1993) Seasonal variation in the energy intake and condition of harp seals: Is there a harp seal morph? Problems for bioenergetic modelling. J Zool, Lond 230:513-528

Renouf D, Noseworthy E (1991) Changes in food intake, mass, and fat accumulation in association with variations in thyroid hormone levels of harbour seals (Phoca vitulina). Can J Zool 69:2470-2479

Renouf D, Noseworthy E, Scott M (1990) Daily fresh water consumption by captive harp seals (Phoca groenlandica). Mar Mamm Sci 6:253-257

Rosen DAS (1991) Maternal Investment and the Ontogeny of Behaviour in the Atlantic Harbour Seal. M.Sc. Thesis, Biopsychology Programme, Memorial University of Newfoundland

Sanford PA (1992) Digestive System Physiology. Edward Arnold, London, UK

Schmidt-Nielsen, K (1983) Animal Physiology: Adaptation and Environment. Cambridge University Press, New York, NY, USA

Schweigert, FJ (1993) Effects of fasting and lactation on blood chemistry and urine composition in the grey seal (Halichoerus grypus). Comp Biochem Physiol 105A:353-357

Stewart, REA (1987) Behavioral reproductive effort of nursing harp seals, Phoca groenlandica. J Mamm 68:348-358

Tedman R, Green B (1987) Water and sodium fluxes and lactational energetics in suckling pups of Weddell seals (Leptonychotes weddellii). J Zool, Lond 212:29-42

Trillmich F (1986) Maternal investment and sex-allocation in the Galapagos fur seal, Arctocephalus galapagoensis. Behav Ecol Sociobiol 19:157-164

Weimerskirch H, Doncaster CP, Cuenot-Chaillet F (1994) Pelagic seabirds and the marine environment: Foraging patterns of wandering albatrosses in relation

to prey availability and distribution. Proc R Soc Lond B 255:91-97

Weimerskirch H, Wilson RP (1992) When do wandering albatrosses Diomedea exulans forage? Mar Ecol Prog Ser 86:297-300

Weisbrodt NW (1985) Gastric motility. In Johnson LR (Ed) Gastrointestinal Physiology, The C V Mosby Company, St. Louis, Missouri, USA

Williams EJ (1959) Regression Analysis. John Wiley and Sons, New York, NY, USA

Wilson RP, Cooper J, Plötz J (1992) Can we determine when marine endotherms feed? A case study with seabirds. J Exp Biol 167:267-275

Wilson RP, Culik BM (1991) The cost of a hot meal: Facultative specific dynamic action may ensure temperature homeostasis in post-ingestive endotherms. Comp Biochem Physiol 100A:151-154

Wilson RP, Puetz K, Bost CA, Culik BM, Bannasch R, Reins T, Adelung D (1993) Diel dive depth in penguins in relation to diel vertical migration of prey: Whose dinner by candlelight? Mar Ecol Prog Ser 94:101-104

Worthy GAJ, Morris PA, Costa DP, Le Boeuf BJ (1992) Moult energetics of northern elephant seals (Mirounga angustirostris). J Zool, Lond 227:257-265